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Mortality in the Patagonian guanaco (Lama guanicoe): can skulls provide accurate estimates of juvenile mortality in the absence of other data?

Jennifer Lynn Donnelly
Iowa State University

Mortality in the Patagonian Guanaco (*Lama guanicoe*): Can skulls provide accurate estimates of juvenile mortality in the absence of other data?

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Jennifer Lynn Donnelly

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Program of Study Committee:
Dean C. Adams, Major Professor
Daniel A. Ashlock
Gavin J. P. Naylor

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Iowa State University

This is to certify that the master's thesis of

Jennifer Lynn Donnelly

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

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Chapter 1: Introduction

1.1 Overview

Estimation of life history parameters is an important part of evolutionary ecology. However, estimation of mortality rates can take decades in long-lived species. Therefore, methods for estimating mortality rates from animal remains are desirable because they enable the researcher to investigate mortality rates over a much shorter period of time. In this study, I investigate whether it is possible to accurately estimate mortality from a population of guanaco (*Lama guanicoe*) skulls in the absence of any other data. I also investigate the problem of missing data from skulls since weather, predation, scavenging, and fire may damage the skulls before collection.

1.2 Principles of Evolutionary Ecology

Ecology was first defined by Ernst Haeckel in the 1860's as the study of the struggle for existence described by Darwin in *On the Origin of Species* (McIntosh 1985). This struggle includes competition with other organisms (Darwin 1859) and the solitary endeavor to survive the abiotic factors of one's environment and reproduce (Wallace 1855). Today, we define the environment to be a mixture of biotic and abiotic factors and adaptation is a result of the struggle against both. For example, Pianka defined organisms' environments as the "totality of the physical and biological factors affecting them or influenced by them" (Pianka 1994, p.5) The major questions of ecology are grounded in the idea of struggle against the environment. Some of the questions generated by this idea are:

1. How do organisms adapt to the biotic and abiotic factors of their environments?

2. How do interacting species coexist and assemble into communities?

3. What are the effects of local adaptation on the morphology and life history traits of a population?

Evolutionary ecology is the study of how organisms interact, adapt to local conditions, and persist through time, influencing such factors as geographic distribution of species and community assembly. The accumulation of adaptations can lead to speciation and shifts in community composition.

1.2.1 Adaptation to Local Environments

Understanding adaptation to the environment spans multiple levels of biological organization, from the individual to the community. Adaptation is a result of natural selection acting on the individual. Taken as a group, the changes wrought by adaptation on individuals bring about changes on the population level, such as in life history parameters like mortality rates. These changes may also be reflected in the morphology of the organism in response to abiotic factors, such as changes in morphology due to extreme currents in demosponges (Bell et al. 2002), or in response to biotic factors such as predation or competition, such as body shape associated with feeding behavior and tooth morphology in cichlid fishes in Lake Tanganyika (Rüber and Adams 2001).

1.2.1.1 Adaptation to Abiotic Environmental Factors

Abiotic factors include weather, physical substrate, and elevation. Rainfall and temperature are very important factors of an organism's environment. If rainfall is low, adaptations to minimize dessication are essential. However, those same adaptations are of no use for life in a tropical rainforest where water is plentiful. A good example of this type of

adaptation is the reduction of leaf size in cacti (Family *Cactaceae*); a reduction in leaf area leads to fewer stomata from which water can be lost. However, large leaf area may be of great importance to a plant competing for light in the canopy of a rainforest, such as *Pourouma bicolor* (Rijkers et al. 2000). Another example of adaptation to climate is the thick fur coat that helps a polar bear (*Ursus maritimus*) survive the extremes of the polar regions. This coat is obviously not appropriate for mammals which reside in the tropics.

Physical substrate also plays a major role in an organism's evolution. While organisms on land and in saline environments both must evolve adaptations to prevent water loss, the nature of those adaptations is necessarily different. While organisms in saline environments must evolve structures to excrete salt to reduce water loss, fresh water organisms must evolve measures to limit water uptake. For example, the shark rectal gland salt tubules help to maintain the osmotic gradient sharks have evolved (Miller et al. 2002) while killifish have evolved different chloride cells for fresh and salt water environments to maintain their osmotic gradient (Katoh et al. 2001).

Another example of the necessity of an adaptation an organism must make is to the elevation of its habitat. Because the air is thinner at high altitudes, organisms that spend time significantly above sea level must evolve hemoglobin with a high affinity for oxygen. An example of this phenomenon is found in the bar-headed goose (*Anser indicus*) which migrates over Mount Everest. The Andean goose (*Chloephaga melanoptera*) which lives at an elevation of 6 km in the Andean Mountains in South America has independently evolved a different form of hemoglobin with a high affinity for oxygen (Golding and Dean 1998).

1.2.1.2 Adaptation to Biotic Environmental Factors

Because resources in a given habitat are finite, interactions with other organisms play a key role in the evolution of a species. These resources may be food, nest sites, mates, sunlight, or any other quantities organisms need to survive and reproduce. The *n*-dimensional hypervolume of ecological variables required for persistence by a species is its fundamental niche (Hutchinson 1957). The species' realized niche is the subset of this hypervolume under which the species actually exists (Pianka 1994). How organisms fill the niche space of a given environment and why there are so many species are major questions in ecology (MacArthur and Levins 1967, MacArthur 1972, Gee and Giller 1987, Futuyma and Moreno 1988, Huston 1994, Kitahara et al. 2000). The concepts of competition and predation partly address this question.

1.2.1.2.1 Competition

Competition occurs when the realized niches of species overlap such that they both require the same limited resource (Birch 1957, Milne 1961). In competitive interactions, whether interspecific or intraspecific, the fitness of one organism or population is negatively impacted by the competition with another individual or population. Organisms compete over food, nest sites, sunlight, water, mates, and other needed resources. The ways organisms have evolved to reduce the effects of niche overlap are of great interest to ecologists (Park 1948, Holt 2003). One such area of study is the tradeoff between generalist and specialist strategies (Pianka 1994). Some organisms adapt generalist strategies which allow them to be flexible in which niches they fill. Others adapt specialized strategies, enabling them to utilize a resource more efficiently. Typically, a generalist is a less effective competitor than a specialist for a

given resource, but specialists tend to be less flexible to changes in their environments. Because generalists can survive under a wider variety of conditions, generalists tend to be more abundant than specialists (Brown 1984). The trade-off between increased habitat flexibility and the ability to more effectively exploit a resource is widespread in nature and is a key factor in the competitive interactions found within a habitat (Cockburn 1991). The evolution of a generalist or specialist life history strategy, or any other trait to reduce competition, can be behavioral or physical.

1.2.1.2.1.1 Physical Adaptations to Competition

One of the most well-known examples of physical adaptations to reduce competition is found in the adaptive radiation in Darwin's finches. These finches have adapted beak shapes and life history traits that have allowed them to colonize a variety of niches on the Galapagos Islands (Darwin 1845, Grant 1986). Examples of the variety of species and their morphological and behavioral adaptations include the woodpecker finch (*Cactospiza pallida*), the medium ground finch (*Geospiza fortis*), and the medium tree finch (*Camarhyncus pauper*). The woodpecker finch has a short, slender beak that can be used to probe woody tissues or use cactus spines and twigs to extract insect larvae from tree branches. The medium ground finch has a short, pointed beak which it uses to forage for ticks on the backs of land iguanas or for crushing seeds. The beak of the medium tree finch is effective for cracking seeds with it's tip (Grant 1986). In a 30-year study of the medium ground finches (*Geospiza fortis*) and cactus finches (*G. scandens*) of the Galapagos Islands, it was found that beak shape changes with variation in the seed availability due to drought (Schluter et al. 1985, Grant and Grant 2002). Hybridization is theorized as the cause of the change in beak shape since the individuals which

were able to survive the changes in food availability. Other species have developed traits for intraspecific competition, particularly for mates. Antlers in red deer (Clutton-Brock et al. 1989) and broad heads with cheek bristles in the Australian platystomadid *Pogonortalis doclea* (Walker) (McAlpine 1975) are used in fights between males for mates and territories. Other mechanisms include copulatory plugs (e.g. funnel web spiders (Masumoto 1993)) and increased body size (e.g. pinnepeds (Lindenfors et al. 2002) and garter snakes (Shine et al. 2000)). In addition, some species have developed phenotypic plasticity as a method to reduce competition (Jordan and Snell 2002). This is particularly noticeable in plants, which are able to modify the direction they are growing to escape shading or crowding.

1.2.1.2.1.2 Behavioral Adaptations to Competition

Behavioral adaptations may evolve in response to intraspecific or interspecific competition pressures. One such behavior is territoriality. Individuals may defend particular resources, such as a food cache or nest site, or may defend a territory to attract mates. In some species, resource defense and mate attraction are inseparable. Male orange-rumped honey guides gain access to mates by defending the nests of giant honeybees to which the females are attracted (Cronin and Sherman 1977). However, in other species, such as the fallow deer (Clutton-Brock et al. 1989), male territories have no function other than to attract mates (Emlen 1968). Territorial defense can be accomplished through signaling, such as singing in white-throated sparrows (Falls 1988) and urination-defecation territorial marking in the Antilopinae, or physical conflict such as in the clashes between male springboks (Walther et al. 1983).

Another method some organisms have evolved to compete is by interfering with another acquiring the desired resource. Sexual interference can take a variety of forms. For example, a

non-territorial male tree frog may intercept a female following the call of a territorial male and "steal" the opportunity to mate (Perrill et al. 1978). Another example is found in salamanders where a male may interrupt the courtship of another male and then mimic the behavior of the female so that the interrupted male deposits a spermatophore without a female to receive it (Arnold 1976). Interference competition can also take place over other resources, such as food. The Argentine ant, an invasive species, uses physical aggression and chemical compounds to drive away native ant species from food sources (Holway 1999).

1.2.1.2.2 Predation and Parasitism

Predation or parasitism occurs when one organism benefits from a reduction in another's fitness (Gotelli 1995). Organisms have evolved numerous physical and behavioral adaptations to avoid predation pressures.

1.2.1.2.2.1 Physical Adaptations to Predation

Physical adaptations which help to evade predation can be found throughout the animal kingdom. Evolution of traits for outrunning predators are seen in a wide variety of taxa (Vaughan et al. 2000, Richardson 2002). Some taxa have evolved toxins and bright coloration, such as monarch butterflies (Ritland and Brower 1991) and poison arrow frogs (Myers 1987), which predators learn to avoid (Pianka 1994). Other organisms, such as the king snake (*Lampropeltis pyromelana*) (Pfennig et al. 2001), have evolved coloration mimicking the warning coloration of poisonous species to deter predators (Batesian mimicry)(Bates 1862). Because a predator is less likely to learn to avoid a particular warning coloration if mimics are more abundant than toxic species, Batesian mimics are generally less numerous than the species they mimic (Pianka 1994). Crypsis, or the ability to blend into one's background, has

evolved to allow organisms to hide from their predators (Benson 1933, Otte and Williams 1972, Moynihan and Rodaniche 1977, Donnelly and Dill 1984, Sauer 1984).

1.2.1.2..22 Behavioral Adaptations to Predation

Behavioral adaptations have also evolved to help species reduce predation pressures. Watchful behavior helps prey detect approaching predators and escape before the predator is close enough to be an immediate danger. Alarm calls by watchers have been observed in many prey species, and can convey information about the approaching predator (Blumstein 2002) as well as let the predator know that it has been spotted surprise (Hasson 1991, Blumstein 2002) . Alarm behavior can also be visual signals (Owings and Hennessy 1984, Caro 1986, Caro et al. 1995) or chemical signals (Krause 1993).

While flocking or aggregating may reduce the amount of food available or make individuals easier to find by predators, this behavior has arisen several times and for a variety of reasons. One common reason is that many individuals are more likely to see an approaching predator than a solitary individual, a phenomenon known as the "many eyes" principal (Alcock 1993). Another reason for forming groups is to decrease the likelihood of being the prey chosen in a given attack by a predator. According to Hamilton's selfish herd theory (Hamilton 1971), predation risk decreases as the individual approaches the center of the group. While this theory holds for some species (Parrish 1989, Krause 1993), the center of the group has a higher risk than the outside others, although this risk is still lower than for solitary individuals (Parrish 1989).

Some prey species will attack their predators. Mobbing behavior has been exhibited in many animals, and has been well studied in birds as a way to reduce predation pressures on eggs and young (Altmann 1956).

A common defense against predation is predator swamping, a phenomenon in which the births in a population are synchronized. Because predators do not have infinite appetites, they can only eat so many of the offspring and the chance that some will survive to reproduce is higher when offspring are born synchronously (Caughley and Sinclair 1994). Another way to swamp predators is through sheer numbers (Cockburn 1991). If many offspring are produced, the probability that some will survive is increased.

1.2.1.3. Apparent Competition and the Keystone Species Concept

Some predators are essential for controlling prey population levels. In some ecosystems, a predator reduces the density of other species to the point that they are able to coexist. When this keystone speices is removed, one species will out compete the other (Paine 1969, Pimm 1980). An example of a system where prey species appear to be in competition, but are actually regulated by a keystone predator is found on the rocky shores of the Pacific Northwest. The ocher starfish (*Pisaster ochraceus*) preys on several species of invertebrates, but prefers the mussel *Mytelus edulis*. While *Pisaster* is present, the community of invertebrates is able to coexist. However, when the starfish is removed, *Mytelus edulis* out competes the other species and a monoculture of the mussel arises (Paine 1966).

1.2.2 Community Assembly

While predation and competition do much to explain how and why species fill a given amount niche space , they are unable to completely answer the question of how species coexist

and assemble to form communities. Community ecology is the study of which species are found in a given environment at a given time and what roles those species play (Law 1999). Which species are present in a community depends on the local processes operating and the species available in nearby geographical locations (Ricklefs 1987, Ricklefs and Schluter 1993). Diamond (1975) proposed that species co-occur in non-random patterns due to competitive interactions. Therefore, of all the possible combinations of species possible for a given habitat, some "forbidden" combinations will never occur while other, "permissible" combinations, will occur more often than if species were distributed at random. Permissible combinations are resistant to invasion by competing species, possibly due to efficient partitioning of resources. Some combinations that do occur may only occur in the presence of a larger group of species. Island size, whether the island is simply a habitat patch or an area separated from the mainland, may also affect the combinations which are permissible. Finally, the combination of multiple permissible combinations may be unstable.

Dispersal mechanisms also play a key role in determining species composition since species which are able to efficiently colonize a habitat and have sufficient population size to do so can occupy an island for a longer time than species which are less efficient dispersers. Law (1999) argues that the central variable in community assembly is the subsets of species in the region which exhibit *persistence*, because they are those which are less likely to have a transient existence in the community. If the persistent species can be quantified, the rate of turnover of the remaining species gives an estimate of the *assembly dynamics*. Although Diamond's rules of community assembly have been contested in the literature (Simberloff and Connor 1979, Strong et al. 1984, Gotelli and Graves 1996), Gotelli and McCabe (2002) found evidence for these rules in a meta-analysis of 96 published species presence-absence matrices.

How generalizable Diamond's community assembly rules are is an open question in ecology and likely to remain controversial for some time to come.

1.3 Population Ecology

An important component of evolutionary ecology is the study of the life cycle of an organism. The life cycle consists of birth, growth, maturation, reproduction, and death. The dynamics of a population or demographics depend on the rates that individuals will undergo each stage of life (Caswell 2001). These dynamics are influenced by time and environment.

Life tables are important demographic tools which have been in use for over a century for studying age-specific life history parameters (Lawless 1982). They do this by recording the number of individuals in each age class at each age and the number of offspring produced at that age. Age-specific mortality and fecundity rates as well as expected lifespan and reproduction can be derived from the mortality and fecundity rates. There are two basic variations of the life table, cohort-specific (also known as age-specific) and time-specific (Caswell 2001). Cohort-specific life tables follow the fates of all the individuals born at a given time throughout their lives. This can be very time-consuming in long-lived species and the model is accurate only for the cohort studied. The time-specific life table exhibits a snapshot of the population structure at a given time and its age specific mortality and fecundity information. If the age-structure and size of the population are constant, the time specific life table can be used to predict future population numbers.

The traditional life table has evenly spaced age intervals and includes age-specific mortality and fecundity information. When the method of age estimation in a population does not produce evenly spaced age groups or major changes in life history occur at irregularly

spaced intervals, life history stages, rather than even age intervals, are used and stage-specific parameters are calculated. When only death data is known, the life table is referred to as being *sensu stricto* (Caswell 2001). This type of life table includes only mortality parameters because fecundity information is unavailable. In this study, the nomenclature and columns of the life table used follow those suggested by Keyfitz (Keyfitz 1968, 1977) and Pielou (1969).

The age interval covers ages (x_i, x_{i+1}), which includes the individuals who died at a minimum of x_i units of age, but before reaching x_{i+1} units of age. Other variables included are n_x, the number of individuals alive in the population in (x_i, x_{i+1}); l_x, the number of survivors at age x standardized to a population size of 1000; d_x, the number dying in (x_i, x_{i+1}); q_x, the age-specific mortality rate for individuals of age (x_i, x_{i+1}); and L_x, the number of time units lived by all individuals alive in (x_i, x_{i+1}). Although population numbers and mortality rates are never stable over evolutionary time, the life table is a useful tool for examining life history parameters over the short term and is widely used by many researchers (Caswell 2001).

One of the disadvantages of studying a long-lived species, such as an ungulate, is the length of a generation. It can take many years to develop accurate estimates of life history parameters such as mortality if the approach is confined to live individuals with known ages. Thus, it is desirable to estimate age from individuals through methods not requiring live specimens. Use of animal remains, such as skulls, may allow us to gain understanding of population structure and dynamics without requiring excessively long field studies.

Animal skulls can provide a great wealth of information to researchers (White 1991). Age estimates may be based on tooth eruption patterns (Raedeke 1979, Larsen and Taber 1980,

Puig and Monge 1983, Sauer 1984), cementum annuli (Raedeke 1979, Larsen and Taber 1980, Sauer 1984), and size (Jaczewski 1991). Changes in the shape of the organism in relation to size (allometry) and age (ontogeny) can also be investigated. From these data, we can gain insight into the growth processes and mortality rates of the population under investigation.

1.4 Morphometrics

The field of morphometrics gives us tools to quantify and analyze patterns of morphological growth and change in a population. Morphometrics is the study of shape variation and its covariation with other variables, such as size and ecological variables. Historically, size and shape have been used for taxonomic classification and understanding of biology, but the ability to rigorously quantify and statistically analyze these traits is a more recent development (Rohlf and Marcus 1993, Bookstein 1998). This enables researchers to test morphological hypotheses to gain deeper understanding of how shape varies with function and why.

1.4.1 Traditional Morphometrics

Traditional morphometrics (Marcus 1990, Reyment 1991), also known as multivariate morphometrics (Blackith and Reyment 1971), evolved as multivariate statistical methods were developed. These methods use sets of linear distances in multivariate analyses as measures of shape for studies of allometry and ontogeny (Jolicoeur 1963). The measured distances should be log transformed since linear distance measures are typically log-normally distributed (Smith 1980). Some of the types of analysis used in traditional morphometrics are the comparison of groups (MANOVA, discriminant function analysis), exploration of variation between and

within groups (PCA, canonical variates, etc), or description of the variation with other variables (multiple regression).

While the evolution of multivariate morphometrics represented an increase in the ability to study size and shape, there are difficulties associated with quantifying morphology using linear distance measures. One difficulty is that size is a large component of a linear distances and must be accounted for in studies of shape. Several methods have been proposed for separating size and shape in linear distance measures, but not all are mathematically equivalent. One such method is to define a measurement a priori to be size, such as snout-vent length in salamanders (Adams and Beachy 2001) or standard length in fish (Cherel et al. 1999). The geometric mean has also been used as an estimate of size. For a matrix of log-transformed measurements, *Y*, the geometric mean is defined as

$$GM_Y = e^{\frac{1}{n}\sum Y}.$$

This mean is based on all measurements for a given specimen, which is less arbitrary than selecting a measurement as size a priori. A third method for estimating size is called 'generalized size' and is calculated from the first principal component (PC1) of a principal components analysis (PCA). This assumes that the elements of the eigenvector that comprises PC1 are all large and positive (Jolicoeur 1984). This is also less arbitrary than selecting a size measurement a priori. However, if the direction of maximal variation in the data is caused by differences between groups, PC1 does not describe size. In addition to PC1, geometric mean, and a priori size measures, several other size measures have been proposed (see Jungers et al. 1995). Unfortunately, because these methods are not mathematically equivalent, choice of size measure affects the results of a study. Also, none of the proposed methods are able to produce

shape variables which are independent of size (Adams et al. 2003). Since at most one measure of size in a linear distance data set is uncorrelated with shape (Mosimann 1970), the confounding of size and shape is a serious problem in traditional morphometrics studies.

A second problem with linear distance measures is the loss of geometry of the anatomical structures being quantified. Without geometry, homology is arbitrarily assigned (Bookstein 1998). For instance, the relationship between the maximum widths of two structures in different organisms are assigned to be homologous, despite the fact that the actual relationship is unknown. Linear distance measures also may be unable to distinguish between shapes. For instance, in Figure 1, the maximum lengths and widths are the same, but the shapes are clearly different. Because the geometry of the structure is lost, a researcher may falsely conclude that the shapes are the same if linear distance measures are used.

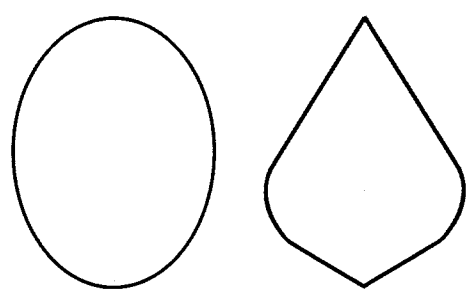

Figure 1: Two shapes with the same maximum length and width which would not be distinguished from these measures.

A final problem with linear distance measures is the inability to graphically depict results. Because the geometry of the structure is lost, results must be summarized in tables. It is much easier to describe shape change from graphical output than from tables of correlations and covariances (Bookstein 1998).

1.4.2 Geometric Morphometrics

The problems with traditional morphometrics, in particular the lack of graphical output, led to a "revolution" in the field of morphometrics in the mid-1980's (Rohlf and Marcus 1993). Rather than using sets of linear distances, methods which characterized shape using alternative data types based on the *x,y* coordinates of landmarks and outlines were proposed. These landmark and outline based methods (*geometric morphometrics*) preserve the geometry of the shape of the organism, making description of differences in shape much more intuitive. Additionally, advances in multivariate shape statistics enabled researchers to combine visualization techniques with rigorous statistical methods (Kendall 1984, 1985, Bookstein 1989, 1991, Small 1996, Dryden and Mardia 1998). A measure of size which is uncorrelated with shape in the absence of allometry was also found. This is centroid size, or the root-summed-squared distance of all landmarks from the centroid (center of gravity for the specimen). Centroid size is defined as

$$C_{size} = \sqrt{\sum_{i=1}^{p} (X_i - X_c)^2},$$

where X_i is the matrix of X,Y coordinates for the landmarks of a specimen, X_c represents the matrix of p copies of the coordinates for the centroid, and p is the number of landmarks. Therefore, centroid size enables researchers to separate size and shape for investigations of allometry (Bookstein 1998).

Several methods to capture the geometry of shape using landmarks were proposed, beginning with the box truss, in which distances between groups of four landmarks are measured (Rohlf and Archie 1978). However, average shapes constructed with this method are

often not coplanar due to measurement error and adjustments must be made to "flatten" the truss (Bookstein et al. 1985). While this method does use landmarks, it does not do so directly; instead, distances between landmarks are used.

Later methods made use of the coordinates of the landmarks rather than distance measures. The general procedure, no matter which method is used, is to remove all non-shape information from the specimens before analyzing shape. Therefore, the specimens are translated to a common location, rotated to a common orientation, and rescaled using centroid size. Using Bookstein's (1986) shape coordinates, or two-point registration, each specimen is translated so that a homologous landmark, A, lies at the origin. A second landmark, B, is rotated to the x-axis. The specimen is then resized so that the distance between A and B is one. While this was an improvement in that landmarks were the data rather than measurements, choice of baseline for size correction had an effect on the results (Bookstein 1991).

Generalized Procrustes Analysis (GPA) is a least-squares superimposition technique that minimizes least squares deviations between corresponding landmarks (Rohlf and Slice 1990). Specimens are translated so that the centroid is at the origin. The specimen is then resized by centroid size. The next step is to iteratively rotate the specimens to minimize the Euclidean distance between corresponding landmarks of each specimen and those of the reference specimen using a least squares criterion (Figure 2). This algorithm is quite fast, usually needing only a few iterations to optimally align the specimens with minimum variation in the data set. The first specimen is chosen as the reference for the first iteration and the average specimen from each iteration is used as the reference for the next iteration. Each

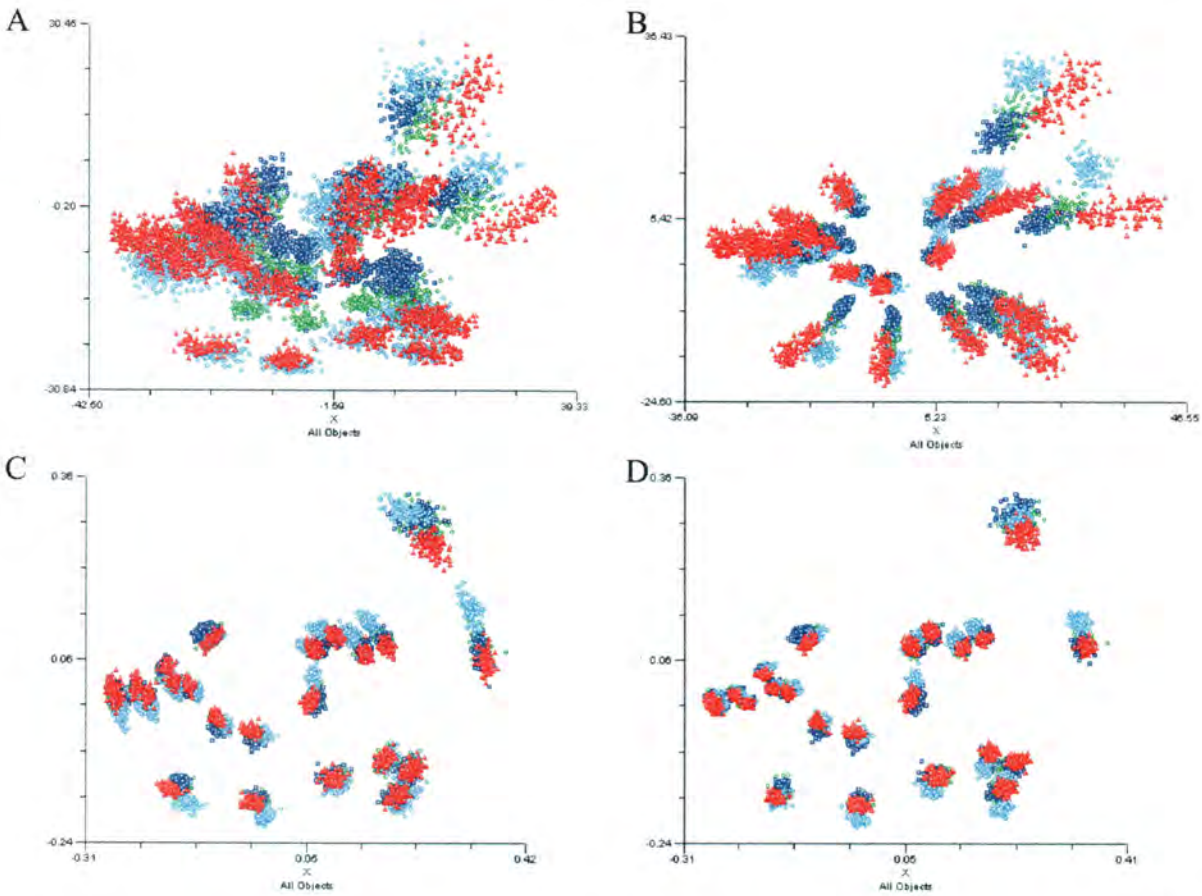

Figure 2: Generalized Procrustes analysis 23 landmarks on 400 stickleback skulls (*Gasterosteus aculeatus*). The red points are from individuals from the limnetic population in Visnaw Lake, the light blue are individuals from the marine habitat of Rabbit Slough, the dark blue individuals are benthic feeders from Mud Lake, and the green individuals are benthic feeders in Meadow Creek. A.) The raw data from digitizing the skulls. B.) The specimens have been translated to a central location to eliminate error caused by location of the skull in the picture. C.) The specimens have been rescaled by centroid size so that size-independent shape can be examined. D.) The translated, rescaled, and optimally rotated specimens. Data from Caldecutt and Adams (1998).

specimen X_i is aligned by assuming that the specimen can be described as the reference specimen with error in each landmark and differences in translation, rotation, and scale. Therefore,

$$X_i = \rho_i (X_0 + E_i) H_i + 1_p \tau_i'$$

where X_0 is the reference, E_i is the matrix of deviations from the reference for specimen *i*, ρ_i is the scaling factor, H_i is the rotation factor, 1_p is a $p \times 1$ vector of 1s, and τ_i' is the transpose of

the coordinates of the centroid of specimen *i*. H_i can be found by taking the singular value decomposition of

$$X_0^t X_i = V \Sigma U^t$$

and replacing Σ with *S*, a diagonal matrix with 1s on the diagonal to eliminate shears and reflections (Rohlf and Slice 1990).

Once the specimens are aligned, they are projected from the curved Procrustes shape space (Slice 2001) to a tangent space using orthogonal projection. This can be accomplished using Burnaby's orthogonal projection (Burnaby 1966) or calculation of the thin-plate spline (TPS) variables and uniform components of shape. Once the data are projected into the tangent space, it is possible to perform statistical analyses on the results of the GPA. Differences in shape can be visualized using TPS, a technique borrowed from engineering which uses deformations in a rectangular grid to show differences in shape between the reference specimen and a given specimen (Figure 3) (Bookstein 1989, 1990, 1991).

1.4.3 Advances in Morphometrics

The field of morphometrics continues to advance quickly, with new variations on the GPA method being proposed to solve particular problems. One such problem was that of outlines. When a study organism lacks repeatable, homologous landmarks or the number of landmarks needed to capture the shape of a specimen requires an excessively large sample size, the outline of the organism may be used to study shape. Until recently, this was performed by elliptical fourier analysis (EFA) (Rohlf 1990). However, new advances in publicly available

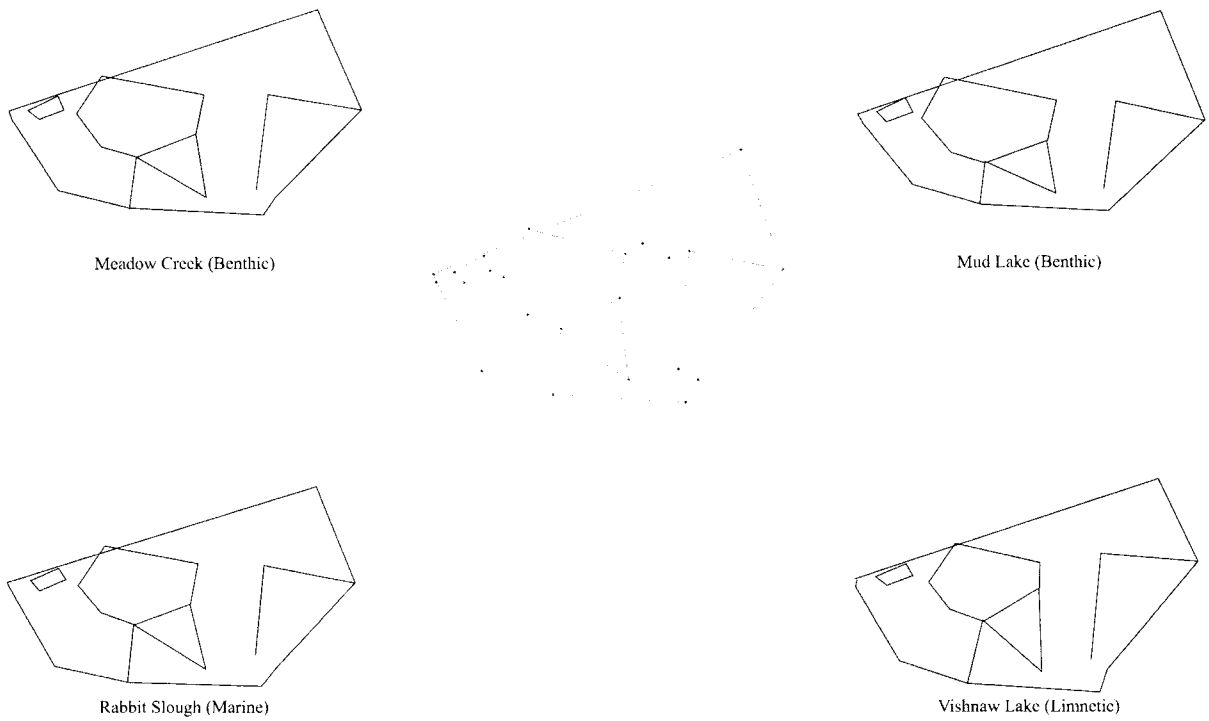

Figure 3: Thin-plate spline deformation grids showing differences between the four populations of stickleback fish in Caldecutt and Adams' study with the overall average (reference) configuration in the center (data from Caldecutt and Adams 1998).

software (TPSrelw (Rohlf 2003)) have enabled researchers to implement the semilandmark concept proposed by Bookstein (Bookstein 1997). In this approach, landmarks that are constrained to lie on a curve are allowed to "slide" along a section of a curve so that the bending energy in a TPS analysis is minimized. An advantage of this method for outlines is that the statistical theory for GPA is much more rigorous than that of EFA. Another advantage of this method is that it allows the combination of landmarks and outlines in a single analysis.

Another problem encountered in morphometric studies is that of articulating structures. An individual with its mouth open occupies a different section of shape space than that same individual with its mouth shut. Adams (1999) investigated three methods for accounting for articulation: separate subsets, fixed angle, and the orthogonal projection method. In the

separate subset method, articulated structures are separated into two subsets, each containing the articulation point. These subsets are then aligned separately and the two subsets of shape variables are combined, with the ratio of the centroid sizes of the subsets as an additional variable for size scaling. In the fixed angle method, articulating structures are set to a uniform arbitrary angle before the structures are aligned. The orthogonal projection method employs determining the distortion due to differences in articulation and removing that vector by orthogonal projection. Adams (1999b) found that performing GPA on the articulating structures separately and then combining the aligned specimens was the preferred method for investigating articulated structures because simulation showed that this method had the highest statistical power of the three methods he investigated and the choice of angles for the fixed angle and orthogonal projection method are arbitrary and affect the results of the study. An additional convenient property of the separate subset method is that it is computationally simple in comparison with the other methods Adams examined.

Other advances in geometric morphometric applications include treating motion as a trajectory through shape space (Slice 1999, 2002), examining fluctuating asymmetry (Klingenberg and McIntyre 1998, Mardia et al. 2000, Kent and Mardia 2001), and quantitative genetics (Klingenberg and Leamy 2001, Klingenberg et al. 2001, Monteiro et al. 2002). Advances are being made in studying estimation of phylogeny (Adams and Rosenberg 1998, Rohlf 1998, Bookstein 2002, Felsenstein 2002, MacLeod 2002, Rohlf 2002), but the fundamental conflict between continuous shape variables and the discrete nature of phylogenies has not yet been resolved (Adams et al. 2003).

One current shortcoming of geometric morphometric tools is that the tools of geometric morphometrics are not robust for the problem of missing data. This is important because structures critical to describing shape in one organism may be missing in another organism. Missing landmarks may be due to damage or morphogenesis, in which the structure has not yet formed. Thus, the number of landmarks which correspond between specimens may vary depending on which specimens are being compared, and the results of a study could vary depending on which subset of specimens was examined.

1.5 Guanacos

Guanacos (*Lama guanicoe*) are members of the camel family (*Camelidae*) found in Argentina, Bolivia, Chile, Paraguay, and Peru (Figure 4) (Torres 1992, CITES Secretariat 2003). They live in arid environments at elevations sometimes exceeding 4,000m (Franklin 1983). According to Charles Darwin, guanacos (Figure 5) are "the characteristic quadruped of the Patagonia... It is an elegant animal in a state of nature, with a long slender neck and fine legs. It is very common over the whole of the temperate parts of the continent, as far south as the islands near Cape Horn. It generally lives in small herds of from half a dozen to thirty in each; but on the banks of the St. Cruz we saw one herd which must have contained at least five hundred." (Darwin 1845)

Guanacos are both grazers and browsers (Franklin 1975), preferring grasses such as *Festuca gracillima* and *F. magellanica* over other types of vegetation. Raedeke (Raedeke 1979) found that consumption of food species by the guanacos of Tierra del Fuego, Chile was correlated with availability and time of year, but that guanacos are not opportunistic foragers. He found that guanacos preferred new growth of forbs and browse when available, but 60% of

their diet consisted of grass and grass-like species. Lichens, fungi, and epiphytes were consumed during the fall when they were most readily available.

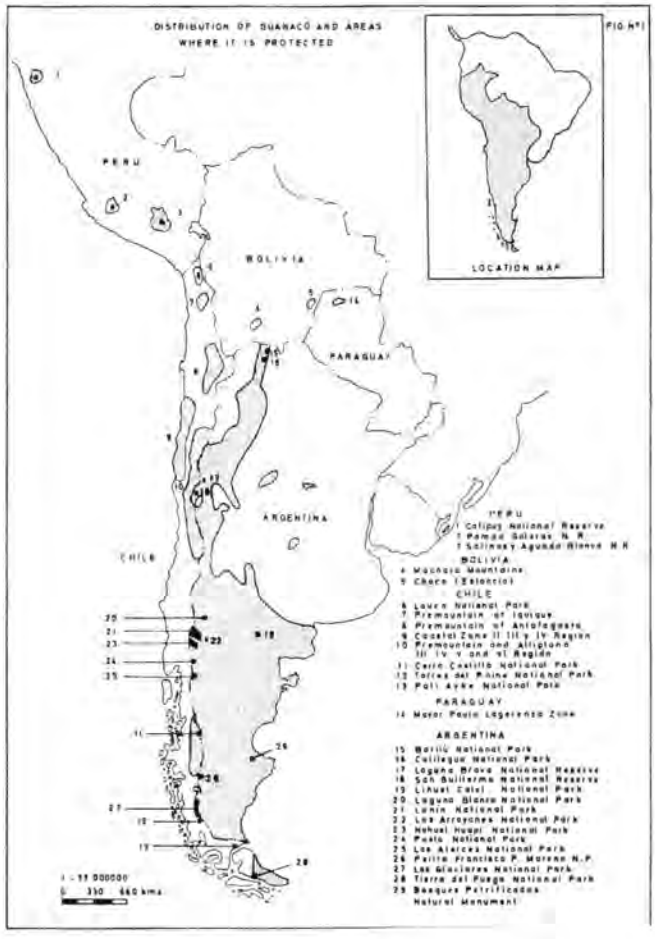

Figure 4: The current distribution of guanacos in South America and where they are protected (from Torres 1992).

Guanacos and domesticated sheep (*Ovis aries*) are competitors for food. When sheep are present, Raedeke (1979) found that guanacos shifted their locations to less preferred areas, causing a shift in their diets. Sheep have more specialized diets and the movement of sheep ranchers and their dogs appeared to displace guanacos. Raedeke also speculates that guanacos would be out competed for food by the sheep without human and canine intervention because of the depletion of the grasses by grazing sheep.

Figure 5: A guanaco family group grazing in Torres del Paine National Park, Chile.

Guanacos are sexually monomorphic, showing sexual dimorphism only in the canine teeth, with the males having large teeth for fighting (Raedeke 1979, Franklin and Johnson 1994). Males exhibit resource defense territoriality (Franklin 1975) and females prefer territories with little cover for pumas (*Puma concolor*) to hide in (Sarno, pers. comm.). Females and their young of the year (chulengos) form family groups and freely move between territories (Franklin 1975). While territorial males may temporarily join family groups, they remain in their territories when the females and their offspring leave. Chulengos remain with their mothers until nearly a year old, at which time they are chased away by the territorial male (Garay et al. 1995). Males that do not have territories are found in large male groups that can number over 100 (Ortega and Franklin 1995).

Predation is a significant component of juvenile mortality. Bank et al. (Bank et al. 2002), Wilson (1984) and Franklin et al (1999) found that pumas preyed preferentially on juveniles. Because so many juveniles are preyed upon, many of their skulls are significantly damaged.

Methods for aging juveniles have traditionally relied on tooth eruption patterns (Raedeke 1979, Puig and Monge 1983, Oporto et al. 1984). However, teeth are often lost after death in

those same processes which damage the skulls, making age estimation by tooth eruption more difficult. An estimator of age which can be applied to damaged skulls is needed if life history parameters are to be estimated from skull populations of guanacos.

Size may be a valuable predictor of age in juveniles of this species. Guanacos undergo approximately 920% growth in the first three years of life. At birth, they weigh approximately 13 kg (Franklin and Johnson 1994). A fully-grown guanaco weighs approximately 120 kg, reaching this full growth at approximately 3 years of age (Raedeke 1979). Shape may also be of value in estimating age since, when studying guanacos in the field, it appears that the skull elongates more than it widens as the animal matures (Figure 6). Therefore, there may be measurable ontogeny in this species which can be applied to the estimation of age.

Figure 6: A mother guanaco and her 15-minute-old chulengo in Torres del Paine National Park, Chile.

Although not all guanaco populations are migratory (Raedeke 1979, Franklin 1983), the guanaco population studied here is migratory (Ortega and Franklin 1995). During the fall, the guanacos migrate in large groups consisting of both sexes across the park to hillier territory which is more sheltered from the elements, but provides greater cover for their primary

predator, the puma (Wilson 1984, Iriarte et al. 1991, Franklin et al. 1999, Sarno et al. 1999, Bank et al. 2002).

The guanaco population studied in this study resided in Torres del Paine National Park (72°55' W, 51°03'S) (Figure 7), a 240,000-ha (Franklin et al. 1999) United Nations Educational, Scientific and Cultural Organization (UNESCO) Biosphere Reserve (UNESCO 2003). Our study area consisted of a "Peninsula" approximately 40 km^2 in size and bounded by Lake Nordenskjöld and the Rio Paine to the north, Lake Pehoe to the west, Lake Sarmiento de Gamboa to the south, and the park border with the Goic sheep ranch to the east (Figure 8). Within the peninsula, elevation ranges from 100 to 300m above sea level (Franklin and Johnson 1994) and the landscape is dominated by Patagonian steppe, which occurs at elevations below 500m (Pisano 1974).

The vegetation of the study area is dominated by mata barrosa (*Mulinum spinosum*), which is a low, rounded, spiny shrub. Mata negra (*Verbena tridens*) is also very prevalent (Franklin et al. 1999) and fills the air with its sweet scent during flowering (personal observation). Other important plant species found in this xeric pre-Andean shrub association are senecio (*Senecio patagonicus*), calafate (*Berberis buxifolia*), and paramela (*Adesmia boronoides*). Woodlands are found at the western end of the study area. Two medium-sized tree species, nirre (*Nothofagus anarctica*) and lenga (*Nothofagus pumilio*) dominate these regions (Texera 1973, Pisano 1974, Ortega and Franklin 1988). In addition to the guanaco, other mammalian species found in Torres del Paine include the Patagonia puma (*Puma concolor patagonica*), which is an important predator in this region (Wood 1981, Wilson 1984, Ortega 1985, Ortega and Franklin 1988, Lawrence 1990, Iriarte et al. 1991, Ortega and

Figure 7: The study site, Torres del Paine National Park, is in southern Chile, near the border with Argentina.

Figure 8: The "Peninsula" area of Torres del Paine National Park, Chile is bounded by the Rio Paine, Lago Nordenskjöld, Lago Pehoe, Lago Sarmiento de Gamboa, and the park boundary with Estancia Goic.

Franklin 1995, Franklin et al. 1999, Sarno et al. 1999, Bank et al. 2002), Geoffrey's cat (*Felis geoffroyi*), the culpeo fox (*Dusicyon culpaeus*), the chilla fox (*D. griseus*), the Patagonia skunk (*Conepatus humboldti*), the European hare (*Lepus capensis*) (Garay and Guineo 1997, Franklin et al. 1999), and the huemul (*Hippocamelus bisulcus*) (Garay and Guineo 1997). Birds species in the park include the Andean condor (*Vultur gryphus*) (Garay and Guineo 1997, Sarno et al. 2000c), crested caracara (*Caracara plancus*), Darwin's rhea (*Rhea pennata*), and several waterfowl and songbirds (Garay and Guineo 1997). Four species of fish and three species of amphibians have been identified in the park as well. According to Garay and Guineo, at least 170 species of insects in 8 families have been identified in the park with additional 6 families which have not yet been identified. Sheep are the primary domesticated animal on the ranches surrounding the park, although ranchers in the area are increasingly switching to cattle in response to world markets (Franklin et al. 1999).

1.6 Project Goals

The primary goal of this study is to investigate what life history information about juvenile guanacos can be gained from a skull population collected in the field. Because skulls are often damaged by predation, the effect of imputation of missing measurements will be investigated. I will investigate how many values can be imputed without introducing significant skew into the data set. A second goal is to determine whether there exists significant allometry or ontogeny in this population and if size or shape are accurate predictors of age. Because the data collected are linear distance measures that are not connected, I will use traditional morphometrics methods to investigate size and shape. If size or shape can be used to predict age in the juvenile guanaco, I will use this data to age skulls for which age

estimation by tooth eruption is not possible. This will increase the sample size for investigations of life history parameters such as mortality rates. I will investigate age-specific mortality in the Torres del Paine guanaco population as an example of information which can be gained from a skull study and to determine whether skull data, in the absence of any other information, is sufficient to estimate mortality in this species.

Chapter 2: Data Collection and Exploration

2.1 Abstract

In this chapter, I describe the methods I used for data collection, exploration, and imputation of missing values. First, the skulls were collected, classified as juvenile or adult, measured, and age estimation of the juvenile skulls by tooth eruption. Second, I imputed values missing due to predator, weather, or fire damage and compared imputed data sets to a data set comprised of skulls that were undamaged. Third, I examined the relationships between size, shape, and age in the juvenile skulls. Finally, I used the information from the relationships between size and age to estimate age in those individuals that were not able to be aged by tooth eruption due to loss of teeth post mortem.

2.2 Data Collection

During the 20 years from 1978 to 1998, 1768 guanaco skulls were collected as they were encountered in the field by guanaco project researchers (Jefferson 1980, Wood 1981, Franklin 1982, Wilson 1982, Jurgensen 1985, Ortega 1985, Garay 1986, Lawrence 1990, Franklin and Fritz 1991, Franklin and Johnson 1994, Garay et al. 1995, Ortega and Franklin 1995, Franklin et al. 1997, Prexl 1997, Sarno 1997, Sarno et al. 1999, Sarno and Franklin 1999, Sarno et al. 2000a, b). These skulls reside in the collection maintained by park officials in Torres del Paine National Park. They are housed in the administrative section of the park.

2.2.1 Measurements Collected

The term *juvenile* is defined and used here as an individual 24 months of age or less. Because all permanent teeth are fully erupted at 24 months of age (Raedeke 1979, Puig and

Monge 1983), all individuals undergoing tooth eruption at the time of death were considered to be juvenile. By this definition, 965 of the collected skulls were identified as juvenile and 392 were identified as adult. The remaining 411 skulls were too badly damaged to determine age class. All juvenile skulls were measured in several dimensions to determine head size and shape. Because of the damage inflicted on some of the skulls by pumas, scavengers, and weather, redundant measurements were taken. The nine measurements taken can be seen in Figure 9. The designations and descriptions of each measurement are listed in Table 1. Both the left and right side of the mandible were measured for COR, CON, and ANG. T-tests were performed on each of these measurements using PROC TTEST in SAS® to ensure that there was not a significant difference between the two sides of the mandible. Because there was no significant difference between the two sides ($p > 0.20$ for all three measurements), the values for the two sides were averaged for those skulls which had measurements for both sides; otherwise, the value from the intact side was used.

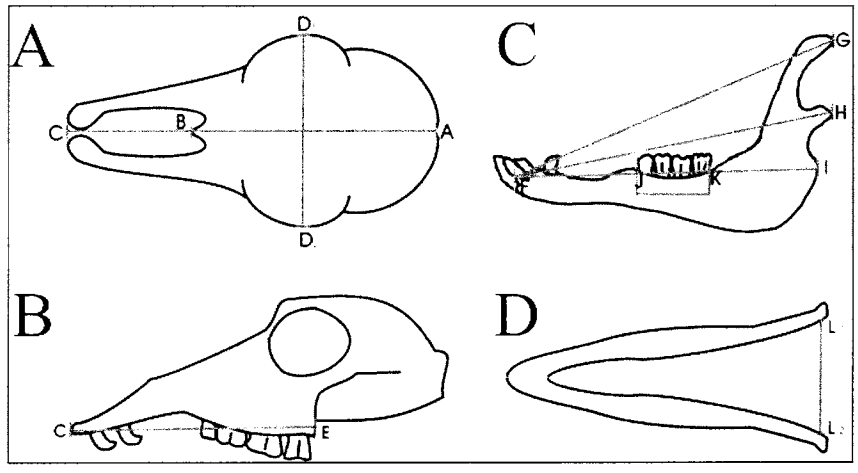

Figure 9: Distances measurements taken for each skull. A) The skull from the superior view. B) Lateral view of the cranium. C) Lateral view of the mandible. D) Superior view of the mandible. See Table 1 for a description of the measurements and their designations.

Variable	Line Designation in Figure 9	Description of Measurement
NAS	AB	The distance from the center of the lambdoidal crest to the anterior tip of the nasal bones. This is an estimate of cranial length.
HLEN	AC	The distance from the center of the lambdoidal crest to the anterior tip of the maxillae. This measurement is used to estimate head length.
ORB	D_1D_2	ORB – The distance between the lateral-most aspects of the orbits. This gives an estimate of head width.
MAXL	CE	The distance from the anterior of the ascending ramus of the maxilla to the anterior tip of the maxilla.
COR	FG	Distance from the posterior-most aspect of the coronoid process to the anterior tip of the mandible. This is another measure of head length.
CON	FH	Distance from the posterior-most aspect of the condyle to the anterior tip of the mandible. This is another measure of head length
ANG	FI	Distance from the posterior-most aspect of the angle to the anterior tip of the mandible. This is another measure of head length.
WCOR	L_1L_2	Distance between the superior-medial-most aspects of the coronoid processes. This is a measurement of head width.
MOLO	JK	Length of the molar opening of the mandible. This was generally taken on the left side of the mandible, where available. When the left side was not present, this measurement was taken on the right side. This measurement may be indicative of age, particularly in animals that have finished growing all of their adult teeth.

Table 1: Guanaco skull measurements, their designations in Figure 9, and their descriptions.

2.2.2 Age Estimation by Tooth Eruption

For estimation of juvenile mortality, mandible tooth eruption patterns were recorded for all 965 juveniles. Teeth were recorded as present or absent, deciduous or permanent, and erupting or fully erupted, as described by Sauer (1984) for white-tailed deer. Since it was not always

possible to tell whether a tooth was lost postmortem, a tooth was recorded as lost if it was absent and the alveolar opening was still present. Due to the fact that alveolar openings are remodeled (close) after tooth loss (White 1991), the tooth was listed as not present if the alveolar opening was not visible or that portion of the mandible was missing. A consensus of the eruption patterns for both sides of each mandible was made to determine the eruption pattern for each individual. Where the two sides of the mandible had different eruption patterns, the side with more usable information for a given tooth (such as one side having a given tooth present while the other had an empty alveolar opening) was used and the side to analyze was chosen at random if the amount of information contained was equal but no consensus could be reached. Mandibles missing too many teeth for accurate age determination were excluded from this portion of the analysis. Age was estimated according to the tooth

Estimated Age	**Patterns Exhibited**								
(Days)	I_1	I_2	I_3	C_1	PM_3	PM_4	M_1	M_2	M_3
30	D	d	-	-	d	d	-	-	-
92	D	d	d	d	d	d	(P)	-	-
217	D	d	d	d	d	d	P	-	-
304	D	d	d	d	d	d	P	(P)	-
457	(P)	d	d	(P)	d	d	P	P	-
546	P	P	(P)	d	d	d	P	P	-
730	P	P	P	P	x	P	P	P	P

Table 2: Mandibular tooth eruption patterns and the average age exhibited by individuals with that pattern (adapted from Raedeke 1979). d=deciduous, P=permanent, ()=erupting, x=tooth lost and not replaced by permanent. I = Incisor, C = Canine, PM = Premolar, M = Molar. Subscripts begin anteriorly and increase as the teeth progress dorsally along the mandible.

eruption schedule from Raedeke (1979) (Table 2). The number of skulls of each age in this data set are shown in Table 3.

Estimated Age (Days)	Frequency
30	8
92	175
217	11
304	97
457	29
546	91
730	2

Table 3: The number of skulls of each age category as estimated by tooth eruption.

2.3 Exploratory Data Analysis

Because linear distance measures are typically log-normally distributed (Smith 1980), all distance measurements were log-transformed. The correlation between each transformed measurement and age was calculated in JMP (SAS Institute 2002). All measurements except WCOR were correlated with age ($r > 0.5$) (Table 4). WCOR was also often missing due to the fragile nature of the tip of the coronoid process. Therefore, WCOR is the only measurement which was not used for the remainder of the analyses.

2.3.1 Imputation of Missing Values

Many of the skulls in this study were damaged, either by predation, scavenging, weather, or fire. Therefore, not all measurements were available for some individuals. Further, due to postmortem tooth loss from the skulls, age could not be obtained for many individuals. All juvenile skulls which had ages estimated from tooth eruption were sorted by the number of

Measurement	Correlation With Age
NAS	0.77394
HLEN	0.78058
ORB	0.51767
MAXL	0.77877
COR	0.69651
CON	0.81773
ANG	0.81969
WCOR	0.05670
MOLO	0.79887

Table 4: Correlations between skull measurements and ages estimated by tooth eruption. Only WCOR is not correlated with age.

measurements present, and eight data sets were compiled from these data (Table 5). The first set contained the 39 skulls which had all eight measurements present. This will be referred to as the *complete* data set. The second set contains the complete set ***AND*** all skulls which were missing only one measurement. This set will be referred to as *data set 7*. The remaining six sets are similarly labeled by the minimum number of measurements present for each skull in the data set. Therefore, they are referred to as *data set n*, where *n* is the minimum number of measurements present.

To obtain estimates for missing values, each data set was mean centered by subtracting the mean for each variable and then dividing by the standard deviation, transforming the data to standard normal deviates. Missing values in data sets 1 through 7 were imputed by PROC MI in SAS (SAS Institute 1999), using a Markov chain Monte Carlo method (multinormal method MCMC), five imputations, and constrained to fall within 2.5 standard deviations of the mean. In this method, SAS performs a regression on the data to estimate missing values. A normal

Data Set	Number of Measurements	Number of Skulls
Complete	8	39
7	≥ 7	89
6	≥ 6	124
5	≥ 5	165
4	≥ 4	268
3	≥ 3	355
2	≥ 2	374
1	≥ 1	412

Table 5: Sample size for each data set and the number of measurements available for each member of that data set.

distribution with the estimate of the missing value as the mean is calculated and a new value is selected at random from this normal distribution to replace the missing value. Each missing value is imputed five times, so that a total of five data sets are created.

Because PROC MI is an experimental procedure in SAS (SAS Institute 2001), a multivariate analysis of variance (MANOVA) was performed on each imputed data set to determine whether SAS was consistent in imputing the missing values. Because the five imputed copies of each data set did not significantly differ, the average value for each measurement for each skull was calculated to create a single data set with imputed values, which will be referred to as *imputed data set n*, where *n* is the minimum number of measurements taken for each skull in the data set.

2.3.2 Statistical Assessment of Imputed Data

Because the imputed values are essentially reasonable guesses for the missing data, it is necessary to determine how many imputed values per skull will introduce skew into the data.

To examine this, each imputed data set was compared to the complete set. This was done with two different methods, MANOVA and cosines of angles in the expectation that agreement between the two analyses will provide strong support for the choice of how many values can be imputed without introducing skew into the data.

2.3.2.1 Assessment of Imputed Data by MANOVA

First, a MANOVA was performed to determine whether each imputed set was significantly different from the complete set. The significance levels from the MANOVAs were examined to determine which imputed data set has the most imputations but was not significantly different from the complete set (Figure 10). As expected, as more values were imputed, the imputed data set diverged from the complete set until, at 4 imputed values, it was significantly different. Therefore, by this measure, no more than 3 values should be imputed to

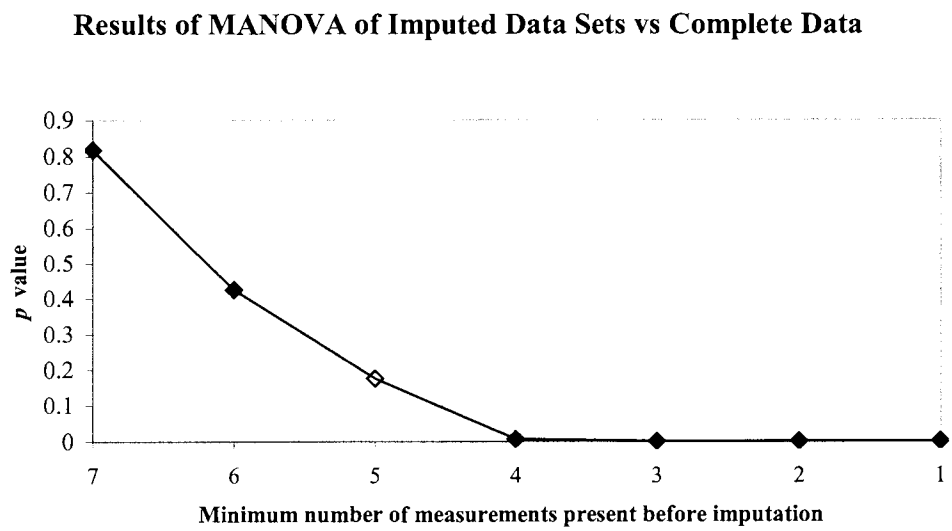

Figure 10: Significance levels from MANOVAs of each imputed data set were examined to determine how many measurements could be missing. The open point (data set 5) represents the largest data set that is not significantly different from the complete data set.

prevent skew in the data and imputed data set 5 is the largest data set which fulfills this restriction.

2.3.2.2 Assessment of Imputed Data by Cosines of Angles

The second method of investigating how many measurements could be missing without introducing skew into the data was examination of the correlation between PC1 of the complete set and PC1 of each imputed data set. To do this, PCA was performed on all 8 data sets and the cosine of the angle between PC1 of each imputed data set and PC1 of the complete set was computed. The cosine of the angle between the first principal component of two data sets is a measure of the correlation between them (Krzanowski 1993). These correlations were examined together to determine which imputed data set appeared to have the most imputed data but did not introduce skew (Figure 11). In general, the correlation drops as more damaged skulls are added, until skulls with at least half their data originally missing are added. At that point, the correlation increases, mostly likely due to the fact that such a high percentage of the data is calculated from regressions based primarily on the complete data set. The correlation for data set 4 gives an upper bound to the correlations of the data sets with more damaged skulls because the imputed values are constrained by the distributions they were selected from, artificially inflating the correlation. Therefore, the increase in correlation for the most damaged three data sets is spurious from a biological perspective. Of those data sets with no skull with more than half its values imputed, imputed data set 5 is the largest data set with a correlation above 0.75.

2.3.2.3 Statistical Assessment of Imputed Data - Conclusions

The two analyses of the number of values which could be imputed without introducing skew into the data showed good agreement. Therefore, the maximum number of values that should be imputed is *n*-3 and imputed data set 5 will be used for further analysis. The age distribution of the skulls in imputed data set 5 is found in Table 6. It is worth noting that despite the fact that this is the largest data set that fulfills the criterion of not introducing skew when missing values are imputed, some age classes, particularly ages 30, 217, and 730 days,

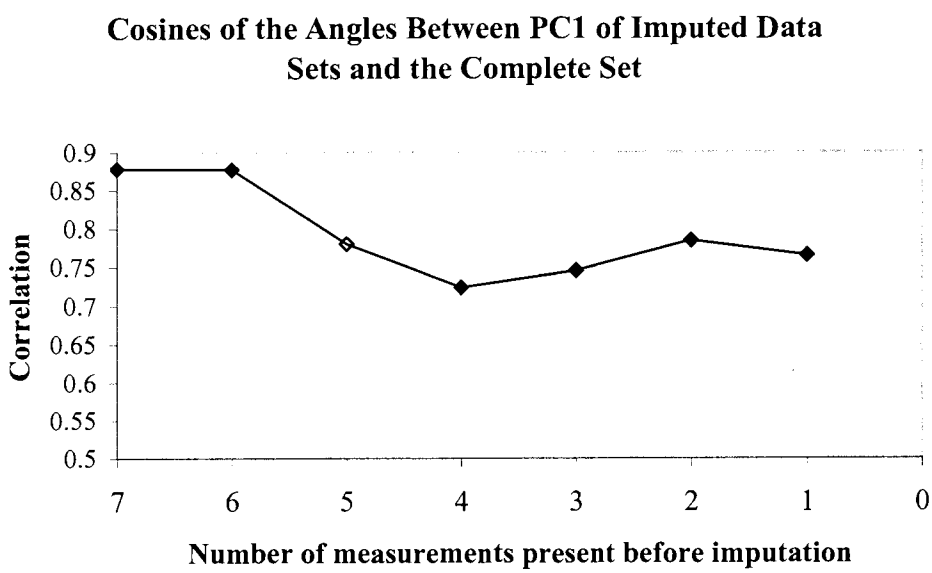

Figure 11: Cosines of the angles (correlations) of PC1 of each data set with the complete set. The open data point, imputed data set 5, is the data set selected as having the largest sample size without introducing skew into the data.

have very small sample sizes. While it would be desirable to have larger samples for these age classes, there is no reasonable way to correct this problem with the data. Because there is no correction for this problem, the data will be used as shown in Table 6.

Age (Days)	Frequency
30	2
92	71
217	4
304	37
457	15
546	34
730	2
Total	**165**

Table 6: Number of skulls of each age found in imputed data set 5.

2.4 Exploration of Variation in Skull Size, Shape, and Their Relationship to Age

Using data from imputed data set 5, variation in the linear distances measured in data set 5 was analyzed by principal components analysis (PCA) (Pearson 1901) in NTSYS-pc (Rohlf 2000). The results of this analysis were used to determine whether PC1 could be used as a size variable and how size, shape, and age are related.

2.4.1 Determination of Size and Shape Variables

PC1, which explains 94.4% of the variation in the data, was used thereafter as an estimate of size because the loadings were all similar and positive, ranging from 0.333 to 0.362. PC2 explained 2.649% of the variation in the data and was taken to be shape since it is orthogonal to the size measure. This axis of variation appears to be a contrast between ORB (0.82) and MOLO (-0.52), with additional emphasis on MAXL (-1.4) and COR (-1.1). This describes a contrast between the increase in head width (ORB) and the molar opening (MOLO)

and snout length (MAXL and COR). The remaining 6 principal components were not examined because each explained less than 1.2% of the variation in the data (Table 7).

Principal Component Axis	% Variation Explained	Cumulative %
1	94.4225	94.4225
2	2.649	97.0714
3	1.1607	98.2322
4	0.8531	99.0853
5	0.6131	99.6984
6	0.1725	99.8709
7	0.1188	99.9897
8	0.0103	>100

Table 7: Percent variation explained by each principal component individually and cumulatively for imputed data set 5.

2.4.2 Allometry

Allometry, or the change in shape with change in size, was investigated by examining the loadings of each variable in PC1. If all variables contribute equally to the size of a specimen, the loading for each variable on PC1 should be $1/\sqrt{p}$, where p is the number of variables (Jolicoeur 1963). Therefore, if growth is isometric in this data set, the loading for each variable should be 0.354. The average loading on PC1 is 0.353. Therefore, the loadings of the eight variables in this data set (Table 8) give evidence of isometry in skull size in this population. Pairwise comparison of the loadings of each variable give evidence of change in shape with size. The largest difference in loadings occurs between ORB (a measure of head width) and CON and ANG, which are estimates of snout length. This is similar to the pattern of shape described by PC2, although the variables estimating snout length differ between the

two axes. Therefore, the investigation of allometry gives weak evidence for the expected elongation of the head as the juvenile grows. Thus, if ontogeny can be detected in this data set, it will be a subtle effect.

Measurement	PC1 Loading
NAS	0.355
HLEN	0.361
ORB	0.333
MAXL	0.359
COR	0.352
CON	0.362
ANG	0.362
WCOR	0.343
Average	**0.353**

Table 8: The loading of each measurement on PC1 gives a measure of the allometry for that variable. All values are similar to the isometric value of 0.354, giving evidence for isometric growth in this data set.

2.4.3 Ontogeny

A regression of shape (PC2) as a function of age was performed to determine whether there was measurable ontogeny (change in shape with age) in this data (Figure 12). The slope from this analysis was examined to determine whether it was significantly different from zero, indicating the presence of ontogeny. The variation in shape appeared to decrease slightly with age. However, the lack of a significant correlation between shape and age does not support this ($r = 0.13$). Therefore, although the study of allometry predicted a slight difference in shape with size, I conclude that there is no measurable relationship between age and shape in this data set.

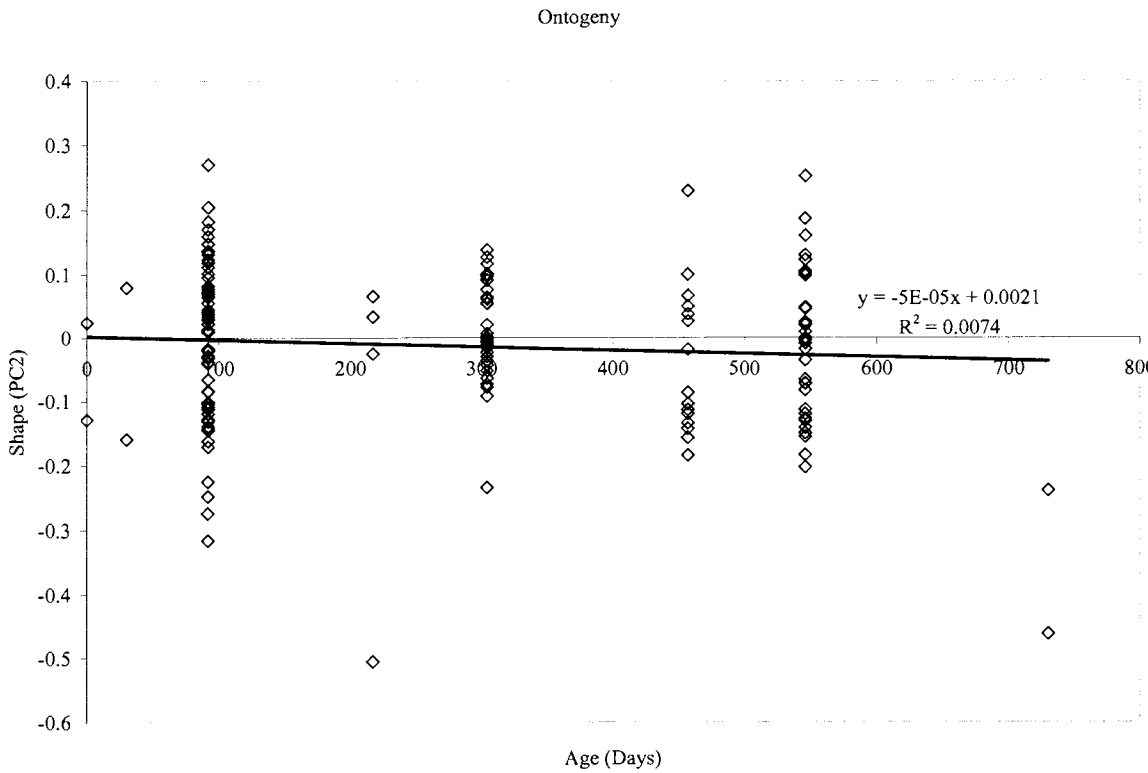

Figure 12: Age was examined as a function of shape (PC2) to investigate ontogeny. Because there is no correlation between age and shape, no ontogeny is present in this data.

2.4.4 Age as a Function of Size

A second regression was performed to determine whether age could be modeled as a function of size. Again, the slope was compared to zero to measure whether age was a linear function of size (Figure 13). Although the relationship is generally found by investigating size as a function of age, size was used as the independent variable in this analysis because it is being investigated as a predictor of age. A significant relationship between age and size was found in this data ($r = 0.777$). Despite the coarseness of the age estimates from tooth eruption, a linear regression of age as a function of size fits the data remarkably well. Because size accounts for more than 94% of the variation in the data, little remains for shape to explain once

size is removed. Therefore, as there is strong evidence for a linear relationship between size and age, but it is not possible to examine the relationship between size and shape in this data

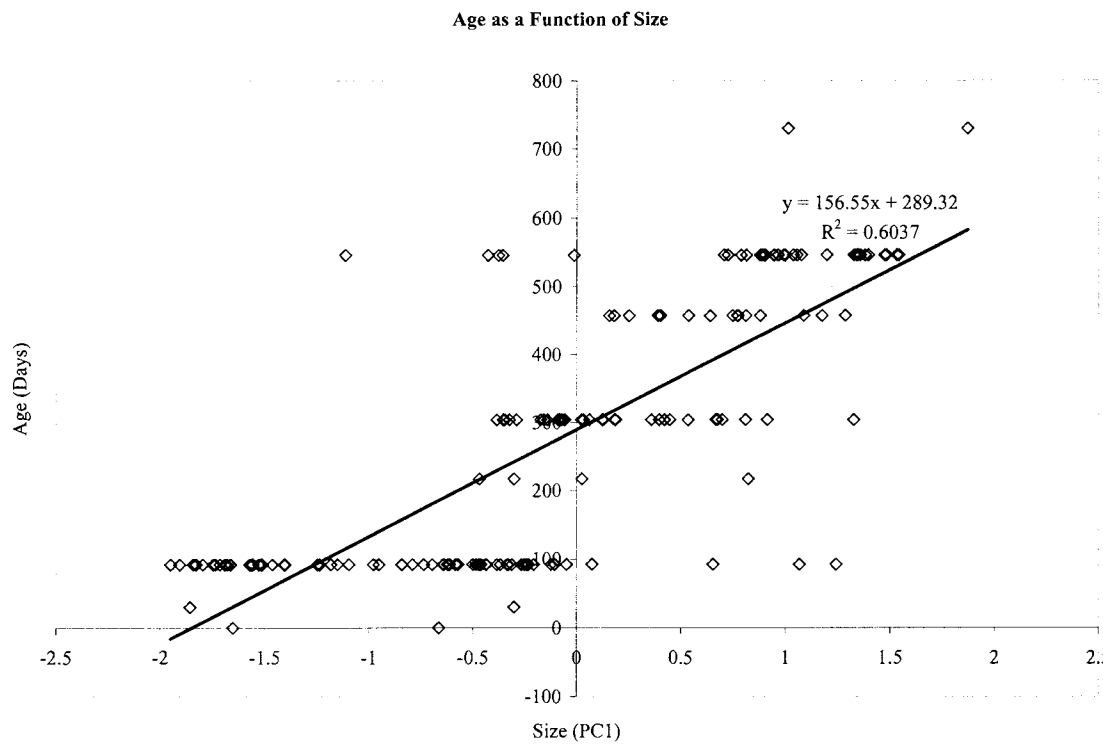

Figure 13: Age is significantly correlated with size in this data, despite coarseness of the age estimates.

due to the mathematical constraint that those axes from PCA are orthogonal (Pearson 1901), I conclude that the evidence for allometry is to weak to reject the hypothesis of isometric growth of the skull and age can be predicted from size in this population.

2.5 Age Estimation From Size

Because the previous analyses implied isometric growth and led to a rejection of the hypothesis of ontogenic allometry in this data, size was used to predict age for those skulls which could not be aged by tooth eruption, but had at least five of the eight measurements

present. The log-transformed measurements for these skulls were converted to standard normal deviates by subtracting off the mean and dividing by the standard deviation as done previously. Missing values were imputed in the same manner as before, using SAS PROC MI with the multinormal method MCMC and limits of ± 2.5 standard deviations. The five imputations were then averaged for each skull to create a complete data set for these unaged skulls. The imputed data was then projected onto PC1 from imputed data set 5 to generate size scores for these skulls. Age estimates were produced from the size scores with the equation from the regression of age onto size.

The addition of the skulls with age estimated from their size increased the size of the data set from 165 to 278, an increase of 68.5% to approximately 28% of the juvenile skulls in the population. Therefore, the fact that nearly three-quarters of the juvenile skulls were too damaged to use in this study, despite the measures taken to recover as many skulls as possible, supports Caughley's (1977) assertion that juvenile skulls are under-represented in "picked up" skull populations. Together with the 392 skulls identified as adults, the skull population for the life history parameter estimation portion of this Thesis numbers 670, which is approximately 38% of the skulls in the collection studied.

Chapter 3: Life Table Analysis and Comparative Mortality Rates

3.1 Abstract

In the previous chapter, I estimated age in guanacos by tooth eruption and compared head size and shape to age to determine whether size and shape can be used to estimate age. I found that estimates of missing values can be accurately imputed if at least five of the eight measurements are present. I also found that age can be predicted from skull size. This allows the estimation of age even when tooth eruption data is incomplete or unavailable. To maximize the sample size for further analysis, I then estimated age for an additional 113 skulls for which tooth eruption data was incomplete. In this chapter, I will pool the individuals aged by tooth eruption and skull size into a single juvenile population and examine mortality rates in this population through life table analysis. I will then compare the age-specific mortality rates I found in the life tables with published mortality rates for the Torres del Paine National Park guanaco population which were estimated by radiocollar study (Sarno et al. 1999) and an earlier skull study (Fritz and Franklin 1994). This allows me to determine whether information from skull data, in the absence of any other information, is sufficient to estimate juvenile mortality in the guanaco.

3.2 Life Table Analysis

Life tables are demographic tools used to examine life history parameters. Two life tables, sensu stricto, were calculated from the aged skull data. The first is a *stage-specific* life table (Table 9), with age listed in days. The age intervals for this life table were determined by the age categories from the tooth eruption study. The second life table, the *yearly* life table (Table 10), has age in years. By calculating the two life tables, it is possible to compare

mortality rates from this skull collection with previously published mortality rates for this population. According to the stage-specific life table, first year mortality peaked between 30 and 92 days of age (1 to 3 months old) and a second peak in mortality occurred between 304 and 457 days of age (10 and 15 months old) (Figure 14). The lowest mortality rates occurred in the first age class and near the end of the second year of life, when the juveniles had nearly attained their full adult growth (Raedeke 1979).

(x_i, x_{i+1})	n_x	l_x	d_x	q_x
0-30	668	1000	7	0.00749
31-91	663	993	118	0.12066
93-217	584	874	51	0.05660
218-304	550	823	64	0.07818
305-457	507	759	115	0.15187
458-546	430	644	54	0.08372
547-730	394	590	3	0.00508
730+	392	587	587	1

Table 9: The stage-specific life table for the Torres del Paine guanaco population. Age is in days. (x_i, x_{i+1}) is the age range; n_x is the number surviving to age x_i, l_x is the number of survivors to age x_i, standardized to a population size of 1000, d_x is the number dying in (x_i, x_{i+1}), and q_x is the age-specific mortality rate for individuals of age (x_i, x_{i+1}).

(x_i, x_{i+1})	n_x	l_x	d_x	q_x
1	668	1000	254	0.25449
2	498	746	159	0.21285
Adult	392	587	587	1

Table 10: The yearly life table for the Torres del Paine guanaco population. Age is in years. (x_i, x_{i+1}) is the age range; n_x is the number surviving to age x_i, l_x is the number of survivors to age x_i, standardized to a population size of 1000, d_x is the number dying in (x_i, x_{i+1}), and q_x is the age-specific mortality rate for individuals of age (x_i, x_{i+1}).

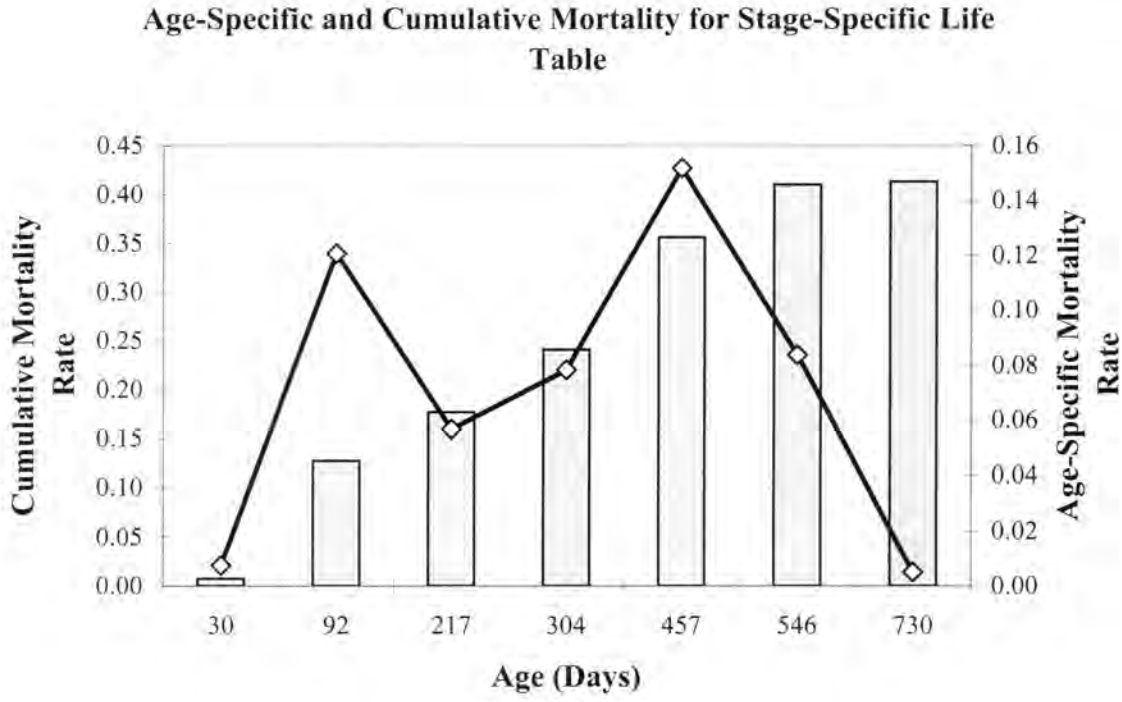

Figure 14: Cumulative and age-specific mortality from the stage-specific life table. The cumulative mortality is in columns and the line and points denote the age-specific mortality

3.3 Comparison of Life Table Results with Published Studies

To determine whether skull data, in the absence of any other information, is sufficient to estimate juvenile mortality in the guanaco, I compared the life table results with the published mortality rates for this population by Sarno et al (1999) and Fritz and Franklin (1994).

From 1991 to 1995, Sarno et al (1999) conducted a radiocollar study on the chulengos in Torres del Paine National Park. Mortality varied by year and the winter of 1995 was particularly severe (Bank et al. 2002). Because Sarno et al's mortality rates for radiocollared individuals (Figure 15) did not significantly differ from those of chulengos without radiocollars, these rates can be taken as estimates of the true mortality rates of this population

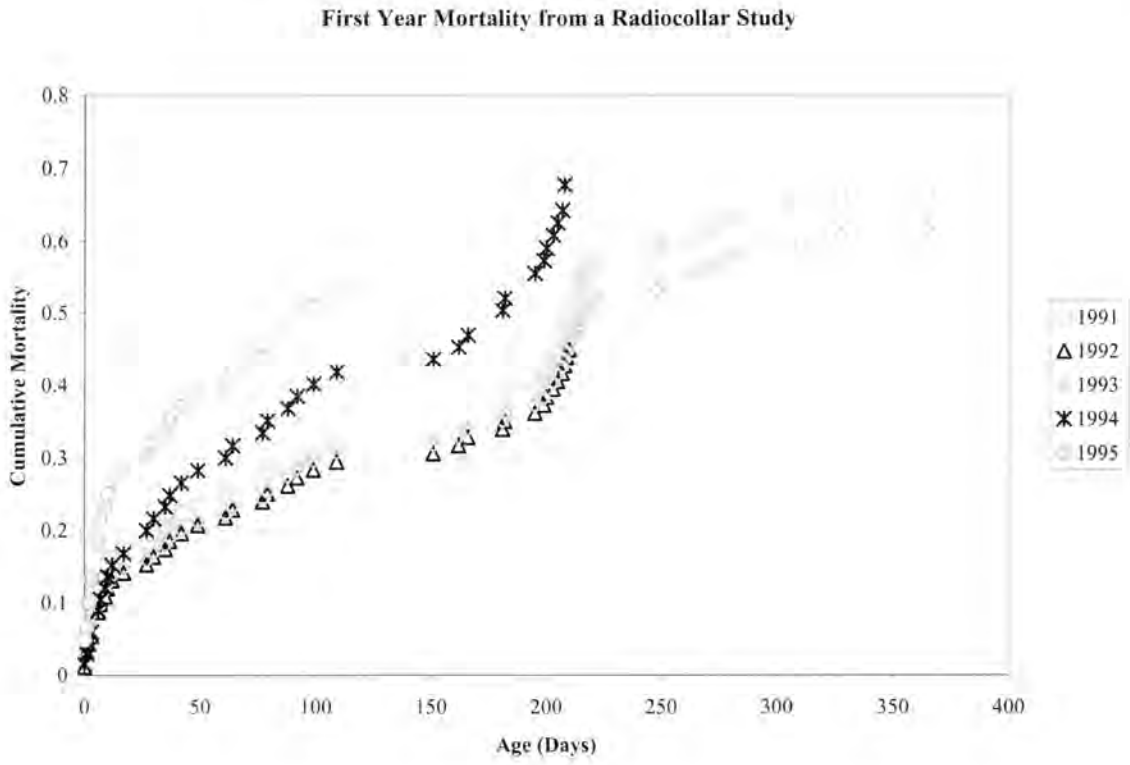

Figure 15: Cumulative mortality rates for the first year of life from Sarno et al's (1999) radiocollar study. 1995 is known to have been a particularly severe winter (Bank et al. 2002). Data from Sarno et al (1999).

(Bank et al. 2000). I pooled the data for all five years of their study into one data set for comparison with the stage-specific life table data and exponentially transformed the data. I also converted the age-specific mortality rates from the stage-specific life table to cumulative mortality rates to match the data Sarno provided to me. To ensure that the transformed data did not violate the assumptions of an ANCOVA, I performed linear regressions on Sarno et al's

data and the stage-specific life table data for the first year of life. Both regressions were significant, and explained the majority of the variation in the data ($r^2 = 0.8118$ and $r^2 = 0.9238$, respectively). I then compared the exponentially transformed mortality rates from Sarno et al's study and the stage-specific life table, via ANCOVA in BIOMstat (Applied Biostatistics 2000), and found that the slopes of the regression lines were significantly different ($p = 0.0045$). Because the life table mortality rates presented here were lower for all age classes than those found by Sarno et al (Figure 16), mortality in this study is underestimated in the first year.

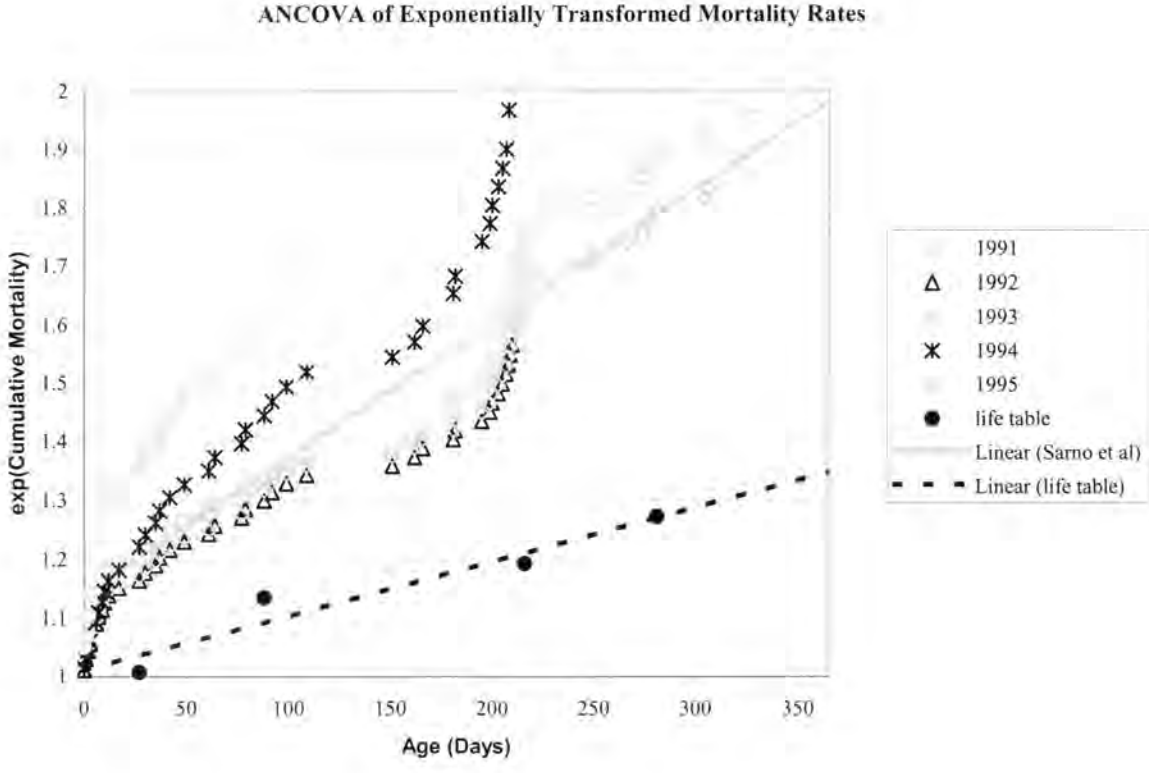

Figure 16: An ANCOVA of the log-transformed mortality rates collected by Sarno et al. (1999) (denoted by years) and the mortality rates from the stage-specific life table. The linear regression of the pooled data for the five years of Sarno et al's study is in grey and the regression of the life table mortality rates is dashed. The slopes of the two data sets are significantly different ($p = 0.0045$), showing that the rates calculated in the stage-specific life table underestimate mortality.

I also compared the rates calculated in the yearly life table to the rates found by Fritz and Franklin (1994) in an examination of the skulls collected in Torres del Paine National Park from 1981-1984 (Table 11). The study by Fritz and Franklin gave higher first year and lower second year mortality than was found in the yearly life table. Differences in the yearly rates between these two studies may be due to several factors. Fritz and Franklin had a smaller sample size (n = 243) for their study, of which approximately 104 were aged 2 years and less. Also, the rates published in their life tables had been adjusted to reflect the assumption that the park population was growing at a steady rate. Finally, Fritz and Franklin had access to necropsy data for some of the skulls collected, which may have influenced their estimates of age (Franklin, pers. Comm.) while the method used to estimate age by tooth eruption in this study is coarse-grained and overestimated the age of some individuals. This is likely to have inflated second year mortality and decreased first year mortality since there is a five-month age gap spanning the end of the first year of life in the life tables calculated herein. Like the mortality rates in this study, Fritz and Franklin's mortality rate for first year mortality is underestimated. This gives further evidence that juvenile mortality will be underestimated in guanaco skull populations.

Age (Years)	Fritz and Franklin	yearly life table
1	0.31	0.254491
2	0.17	0.212851

Table 11: Yearly mortality rates for the study published by Fritz and Franklin (1994) and the yearly life table in this study. Fritz and Franklin found higher first year mortality and lower second year mortality than was found in this study.

Chapter 4: Conclusions

An important component of ecology is the estimation of life history parameters such as mortality rates. These rates can be used to investigate whether the numbers of a species are increasing or declining, whether a species is affected by the presence of other species, and whether an active role for the preservation of the species is necessary. When studying long-lived organisms such as the guanaco, it is desirable to have a method of determining age-specific mortality which does not depend on decades-long studies. Skulls are enduring records of organisms and provide insights into the lives of the organisms and require less time to study. However, skulls found in the field are often damaged by weather, fire, scavengers, and predators. This leads to reduced sample sizes for mortality studies based on skull features, and can also lead to biases in age-specific mortality rates since juvenile skulls are smaller and more fragile.

I began Chapter 2 by explaining the methods I used to collect data from guanaco skulls in Torres del Paine National Park, Chile. Nine measurements were taken on each skull and tooth eruption data was recorded. Eight of the measurements were significantly correlated with age as estimated by tooth eruption patterns. The measurement which was not correlated with age, WCOR, was discarded. In addition to being uncorrelated with age, WCOR was often absent because of the fragile nature of the coronoid processes.

Because many of the skulls I studied were damaged by predation, scavenging, weather, and fire, I was unable to take some measurements for these skulls. Only 39 of the skulls for which I was able to estimate age by tooth eruption had all eight measurements available.

Therefore, it was necessary to investigate the problem of missing data in this skull study to determine if I could increase my sample size. I used the experimental procedure PROC MI in SAS to impute the missing values and examined the data to determine how many measurements were required to prevent the introduction of skew into the data by imputation of missing values. I found that skew was introduced if more than three measurements were imputed. This conclusion is supported by two methods of statistically analyzing the results. I performed a MANOVA on each imputed data set and examined the significance levels. I then determined the cosines of the angles between PC1 of the complete data set and PC1 of each imputed data set, which is a measure of correlation. Both of these analyses supported using data with no more than three imputed values. Therefore, I conducted the remainder of the analyses on imputed data set 5, which had a sample size of 165.

For estimation of age from skulls for which tooth eruption was unavailable or incomplete, I examined size as a predictor of age. Because size and age are significantly correlated, I performed a regression of age as a function of size. I then used this regression and the PC1 score (size) to determine age for those skulls with incomplete or missing tooth eruption data. By estimating age for these additional skulls, I was able to increase the sample size of aged skulls by 65% from 165 to 278 for determining juvenile mortality rates.

In Chapter 3, I investigated whether the data from skulls, in the absence of other information, give adequate estimates of mortality rates in juveniles. I examined this by calculating life tables from the skull study and comparing the age-specific mortality and cumulative mortality rates to the rates in two previously published mortality studies of juvenile guanacos from the same population. The first study, by Sarno et al (1999), used radiocollars to

investigate mortality in the first year of life. Because there was no difference between the mortality of radiocollared individuals and those without collars, Sarno et al's mortality rates approximate the true mortality rates in this population. Although the mortality rates differed by year, they followed a consistent pattern. Mortality was highest just after birth and again at approximately the start of the winter. Because of the coarse-grained nature of my age estimation, my data did not show these periods of high risk in the guanaco's first year of life. Also, I expected, a priori, that my estimates of cumulative mortality would approach estimates by Sarno et al as the individuals got older. Because there were many very young disarticulated skulls in this collection, I expected my mortality rates for the very youngest age class to be low. However, as the animals age, their skulls become more robust and I expected that my estimates of mortality would approach the true mortality rates. However, this was not the case. The slope of the regression line for the age-specific life table data was actually shallower than the slope of the regression line for Sarno et al's data. This may be due to the coarse-grained nature of age estimation by tooth eruption. Because the age class which spans the end of the first year of life in the age-specific life table is five months long, it may be that the age of some individuals which died in their first year of life was overestimated This inflated the mortality rates of the second year and reduced the mortality rates for the end of the first year.

The second previously published study to which I compared my estimates of mortality was by Fritz and Franklin (1994). These researchers also conducted a skull mortality study in Torres del Paine National Park, but they examined yearly mortality throughout the entire lifespan of the guanaco. Fritz and Franklin found a higher mortality rate for the first year of life and a lower rate for the second than I found in the yearly life table. Again, the second year

mortality rate from the yearly life table may have been inflated in comparison due to the coarse-grained nature of age estimation in this study. Also, Fritz and Franklin had a much smaller sample size, with only 243 individuals for the >10 year life span of the guanaco, of which approximately 104 were two years old or less as compared to the 278 individuals of age two or less examined in Chapter 3. The differences in sample size may have contributed to the differences between their study and the yearly life table calculated herein. Also, Fritz and Franklin had access to necropsy data which likely contributed to a greater degree of accuracy in their age estimation in juveniles.

Both skull-based studies had first year mortality rates significantly lower than those found by Sarno et al. This gives strong evidence that Caughley's (1977) assertion that skull studies underestimate juvenile mortality is correct for the guanaco. Because juvenile skulls are smaller and more fragile than adult skulls, the amount of information which can be discerned from juvenile skulls is also reduced. In addition, in this skull collection it appeared that skull sutures do not fuse until some time after birth, so the skulls of newborns disarticulate when the skin and muscle are removed. Thus, newborn mortality is completely missed by studies based on skull size. Also, the bones are very fragile, so very few survive intact enough to provide tooth eruption data. This explains why, if pumas prefer juvenile guanaco prey as found by Bank et al (2002), the high initial mortality due to puma predation (Figure 17) was not seen in the life tables I calculated.

From my study of juvenile guanaco skulls, I conclude that it is possible to estimate missing skull size measurements for a population of guanacos if there are skulls available for which all measurements are available, it is possible to use skull size to estimate age in juvenile

guanacos, and skull information alone is not sufficient to accurately estimate juvenile mortality in this study.

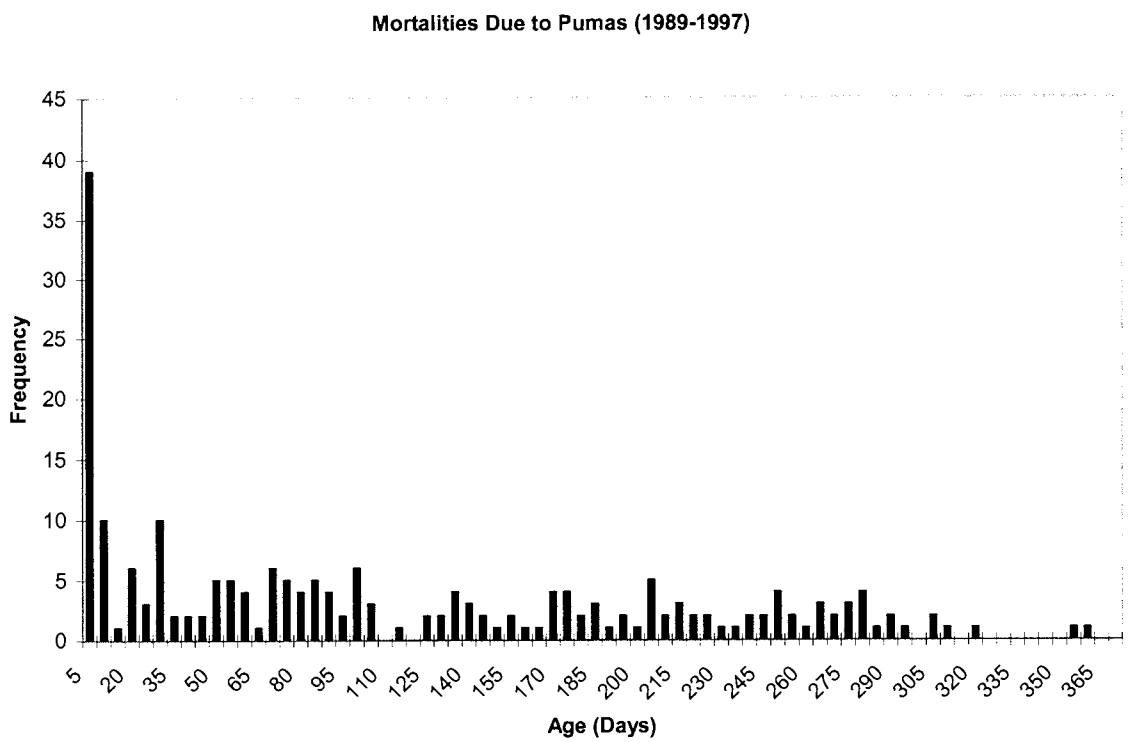

Figure 17: Guanaco mortality due to puma predation in the first year of life in Torres del Paine National Park, Chile (Franklin, unpublished data).

Other variables which, if known, would be beneficial to the study of mortality include location of the skull in the field, date found, sex, cause of death, and weather conditions. Location may play a part in determining climactic factors and possibly the cause of death. Spatial variation may be analyzed to determine whether some parts of the habitat are inherently more hazardous to certain age classes. Because guanacos exhibit synchronous birth (Raedeke 1979, Franklin 1982, 1983), the date the skull was found may give a more accurate estimate of age at death than tooth eruption if the individual was newly deceased. Sex may play an important role in determining hazard in the first two years of life in the guanaco since male

guanacos are expelled from their natal groups earlier than females and are found in male groups rather than family groups after this expulsion (Raedeke 1979, Franklin 1982, 1983, Ortega 1985, Ortega and Franklin 1988, 1995, Sarno 1997, Sarno et al. 1999). Male and female juveniles also exhibit different patterns of behavior leading up to their expulsion from their natal groups (Sarno 1997), which also may affect mortality. Cause of death helps to identify the hazards faced by juvenile guanacos. Because pumas preferentially prey on juveniles (Wilson 1984, Sarno et al. 1999, Bank et al. 2002) and often significantly damage the skulls, quantification of puma predation rates may be useful in predicting mortality rates. If it is known what percentage of the juveniles fall prey to pumas each year, it may be possible to estimate the number dying each year from the deaths due to other causes. Finally, weather plays a significant role in mortality rates for a given year (Gilbert et al. 1970, Jedrzejewski et al. 1992, Bank et al. 2002). In 1995, the winter in Torres del Paine National Park was particularly severe, with very high snowfall, low temperatures, and strong winds. The park suffered the worst winter storm in 50 years that winter, and mortality of juvenile guanacos was significantly higher than expected (Bank et al. 2002). Information of this type, combined with what can be collected directly from the skull gives a more robust picture of mortality and is likely to give a more accurate estimate of mortality rates in juvenile guanacos.

Future work suggested by the results of this study include combining skull mortality studies as listed above with other sources of data and an investigation of the relationship between shape and size. A geometric morphometric study based on landmarks would be useful for examining the relationships between shape, size, and age. I would suggest that this study be conducted on images of live specimens so that changes in individuals can be examined as

the animals age and so that the shape of newborn individuals can be captured without the problem of skull disarticulation. I would also recommend performing the study on skulls so that changes in the skull shape which are hidden by skin and muscle can also be examined. From this study, it would be possible to gain a clearer understanding of how the skull grows in juvenile guanacos. This knowledge could be used to estimate age and, when combined with other ecological data, give greater insight into the first two years of life of a guanaco.

References

Adams, D. C. 1999a. Methods for shape analysis of landmark data from articulated structures. Evolutionary Ecology Research **1**:959-970.

Adams, D. C. 1999. Ecological character displacement in *Plethodon* and methods for shape analysis of articulated structures. PhD thesis. State University of New York at Stony Brook, Stony Brook.

Adams, D. C., and C. K. Beachy. 2001. Historical explanations of phenotypic variation in the plethodontid salamander *Gyrinophilus porphyriticus*. Herpetologica **57**:353-364.

Adams, D. C., F. J. Rohlf, and D. E. Slice. 2003. Geometric Morphometrics: Ten Years of Progress Following the 'Revolution'. Italian Journal of Zoology **in press**.

Adams, D. C., and M. S. Rosenberg. 1998. Partial warps, phylogeny, and ontogeny: a comment on Fink and Zelditch (1995). Systematic Biology **47**:168-173.

Alcock, J. 1993. Animal Behavior. Sinauer Associates, Sunderland, Mass.

Altmann, S. A. 1956. Avian mobbing behavior and predator recognition. The Condor **58**:241-253.

Applied Biostatistics. 2000. BIOMstat: Statistical Software for Biologists. *in*. Applied Biostatistics, Inc., Port Jefferson, NY.

Arnold, S. J. 1976. Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculataum, Ambystoma tigrinum* and *Plethodon jordani*. Zeitschrift fur Tierpsychologie **42**:247-300.

Bank, M. S., W. L. Franklin, and R. J. Sarno. 2000. Assessing the effect of radiocollars on juvenile guanaco survival. Oecologia **124**:232-234.

Bank, M. S., R. J. Sarno, N. K. Campbell, and W. L. Franklin. 2002. Predation of guanacos (*Lama guanicoe*) by southernmost mountain lions (*Puma concolor*) during a historically severe winter in Torres del Paine National Park, Chile. Journal of Zoology **258**:215-222.

Bates, H. W. 1862. Contributions to an insect fauna of the Amazon Valley. Transactions of the Linnean Society **23**:495-566.

Bell, J. J., D. K. A. Barnes, and J. R. Turner. 2002. The importance of micro and macromorphological variation in the adaptation of a sublittoral demosponge to current extremes. Marine Biology **140**:75-81.

Benson, S. B. 1933. Concealing coloration among some desert rodents of the southwestern United States. Univ. Calif. Publ. Zool. **40**:1-70.

Birch, L. C. 1957. The meanings of competition. American Naturalist **91**:5-18.

Blackith, R. E., and R. A. Reyment. 1971. Multivariate Morphometrics. Academic Press, Inc., New York.

Blumstein, D. T. 2002. The evolution of functionally referential alarm communication: Multiple adaptations; multiple constraints. Evolution of Communication **3**:135-147.

Bookstein, F. L. 1986. Size and shape spaces for landmark data in two dimensions. Statistical Science **1**:181-242.

Bookstein, F. L. 1989. "Size and Shape": a comment on semantics. Systematic Zoology **38**:173-180.

Bookstein, F. L. 1990. Higher-order features of shape change for landmark data. Pages 237-250 *in* F. J. Rohlf and F. L. Bookstein, editors. Proceedings of the Michigan Morphometrics Workshop. University of Michigan Museum of Zoology, Ann Arbor.

Bookstein, F. L. 1991. Morphometric tools for landmark data. Cambridge Press, Cambridge.

Bookstein, F. L. 1997. Landmark methods for forms without landmarks: localizing group differences in outline shape. Medical Image Analysis **1**:225-243.

Bookstein, F. L. 1998. A hundred years of morphometrics. Acta Zoologica **44**:7-59.

Bookstein, F. L. 2002. Creases as morphometric characters. *in* N. MacLeod and P. L. Forey, editors. Morphology, Shape, and Phylogeny. Taylor and Francis, London.

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. J. Humphries, G. R. Smith, and R. Strauss. 1985. Morphometrics in Evolutionary Biology: The Geometry of Size and Shape Change, With Examples From Fishes. The Academy of Natural Sciences of Philadelphia, Philadelphia.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist **124**:255-279.

Burnaby, T. P. 1966. Growth-invariant discriminant functions and generalized distances. Biometrics **22**:96-110.

Caldecutt, W. J., and D. C. Adams. 1998. Morphometrics of the trophic osteology in the threespine stickleback, *Gasterosteus aculeatus*. Copeia **1998**:827-838.

Caro, T. M. 1986. The functions of stotting in Thompson's gazelles: Some tests of the predictions. Animal Behaviour **34**:663-684.

Caro, T. M., L. Lombardo, A. W. Goldizen, and M. Kelly. 1995. Tail-flagging and other antipredator signals in white-tailed deer: New data and synthesis. Behavioral Ecology **6**:442-450.

Caswell, H. 2001. Matrix Population Models, Second Edition edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Caughley, G. 1977. Analysis of Vertebrate Populations. Wiley, London.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife Ecology and Management. Blackwell Science, Cambridge, Mass.

Cherel, Y., S. Waugh, and S. Hanchet. 1999. Albatross predation of juvenile southern blue whiting (*Micromesistius australis*) on the Campbell Plateau. New Zealand Journal of Marine and Freshwater Research **33**:437-441.

CITES Secretariat. 2003. CITES-listed species database. *in*. Convention on International Trade in Endangered Species of Wild Fauna and Flora.

Clutton-Brock, T. H., M. Hiraiwa-Hasegawa, and A. Robertson. 1989. Mate choice of fallow deer leks. Nature **340**:463-465.

Cockburn, A. 1991. An Introduction to Evolutionary Ecology. Blackwell Scientific Publications, Boston.

Cronin, E. W., Jr., and P. W. Sherman. 1977. A resource-based mating system: the orange-rumped honey guide. Living Bird **15**:5-32.

Darwin, C. 1845. Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of HMS BEAGLE Round the World. E. P. Dutton & Co., New York.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. J. Murray, London.

Diamond, J. 1975. Assembly of Species Communities. Pages 342-444 *in* J. Diamond and M. L. Cody, editors. Ecology and Evolution of Communities. Belknap, Cambridge.

Donnelly, W. A., and L. M. Dill. 1984. Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate color preference and achromatic reflectance. Journal of Fish Biology **25**:183-195.

Dryden, I. L., and K. V. Mardia. 1998. Statistical Shape Analysis. John Wiley & Sons, New York.

Emlen, J. M. 1968. Optimal choice in animals. American Naturalist **102**:385-390.

Falls, J. B. 1988. Does song deter territoirial intrusion in white-throated sparrows (*Zonotrichia albicollis*)? Canadian Journal of Zoology **66**:206-211.

Felsenstein, J. 2002. Quantitative characters, phylogenies, and morphometrics. *in* N. MacLeod and P. L. Forey, editors. Morphology, Shape, and Phylogeny. Taylor and Francis, London.

Franklin, W. L. 1975. Guanacos in Peru. Oryx **13**:191-202.

Franklin, W. L. 1982. Biology, ecology, and relationship to man of the South American camelids. Pages 457-489 *in* M. A. Mares and H. H. Genoways, editors. Mammalian biology in South America. Pymatuning Laboratory of Ecology and University of Pittsburgh, Special Publication Series, Linesville, PA.

Franklin, W. L. 1983. Contrasting socioecologies of South America's wild camelids: the vicuna and the guanaco. Pages 573-629 *in* J. K. Eisenberg and D. G. Klieman, editors. Advances in the study of mammalian behavior. American Society of Mammologists.

Franklin, W. L., M. Bas, C. F. Bonacic, C. Cunazza, and N. Soto. 1997. Striving to manage Patagonia guanacos for sustained use in the grazing agroecosystems of southern Chile. Wildlife Society Bulletin **25**:65-73.

Franklin, W. L., and M. A. Fritz. 1991. Sustained harvesting of the Patagonia guanaco: is it possible or too late? *in* K. Redford and J. Robinson, editors. Neotropical wildlife use and conservation. University of Chicago Press, Chicago.

Franklin, W. L., and W. E. Johnson. 1994. Hand capture of newborn open-habitat ungulates: the South American guanaco. Wildlife Society Bulletin **22**:253-259.

Franklin, W. L., W. E. Johnson, R. J. Sarno, and J. A. Iriarte. 1999. Ecology of the Patagonia mountain lion, *Felis concolor patagonica*, in southern Chile. Biological Conservation **90**:33-40.

Fritz, M., and W. L. Franklin. 1994. First estimates of guanaco male group harvestability in the Patagonia of South America. Vida Silvestre Neotropical **3**:84-90.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecological Systems **19**:207-223.

Garay, G. 1986. Desarrollo del comportamiento social infantil del guanaco (*Lama guanicoe*). Pontificia Universidad Catolica de Chile, Santiago, Chile.

Garay, G., W. L. Franklin, R. J. Sarno, and W. E. Johnson. 1995. Development of juvenile guanaco social behavior: first study on a wild population from the Chilean Patagonia. Revista Chilena de Historia Natural **68**:429-438.

Garay, G., and O. Guineo. 1997. Conociendo la Fauna de Torres del Paine, 2nd edition. Los Talleres del Instituto Don Bosco, Punta Arenas, Chile.

Gee, J. H. R., and P. S. Giller. 1987. Organization of communities: past and present. Blackwell, Oxford.

Gilbert, P. F., O. C. Wallamo, and R. B. Gill. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. Journal of Wildlife Management **34**:15-23.

Golding, G. B., and A. M. Dean. 1998. The structural basis of molecular adaptation. Molecular Biology and Evolution **15**:355-369.

Gotelli, N. J. 1995. A Primer of Ecology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Gotelli, N. J., and G. R. Graves. 1996. Null Models in Ecology. Smithsonian Institution Press, Washington, D. C.

Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. Ecology **83**:2091-2096.

Grant, P. R. 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton, New Jersey.

Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science **296**:707-711.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology **31**:295-311.

Hasson, O. 1991. Pursuit-deterrent signals: Communication between prey and predator. Trends in Ecology and Evolution **6**:325-329.

Holt, R. D. 2003. On the evolutionary ecology of species' rangers. Evolutionary Ecology Research **5**:159-178.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology **80**:238-251.

Huston, M. A. 1994. Biological Diversity: the Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology **22**:415-427.

Iriarte, J. A., W. E. Johnson, and W. L. Franklin. 1991. Feeding ecology of the Patagonia mountain lion in southernmost Chile. Revista Chilena de Historia Natural **64**:145-156.

Jaczewski, Z. 1991. Remarks on the size of the European moose *Alces alces* L. Pages 307-310 *in* Transactions: 18th Congress on the International Union of Game Biologists, Krakow, Poland.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, and A. L. Ruprecht. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of Bialowieza National Park, Poland. Oecologia (Berl.) **90**:27-36.

Jefferson, R. T. 1980. Size and spacing of sedentary guanaco family groups. MS. Iowa State University, Ames, IA.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics **19**:497-499.

Jolicoeur, P. 1984. Principal components, factor-analysis, and multi-variate allometry - a small sample direction test. Biometrics **40**:685-690.

Jordan, M. A., and H. L. Snell. 2002. Life history trade-offs and phenotypic plasticity in the reproduction of Galapagos lava lizards (*Microlophus delanonis*). Oecologia **130**:44-52.

Jungers, W. L., A. B. Falsetti, and C. E. Wall. 1995. Shape, relative size, and size-adjustments in morphometrics. Yearbook of Physical Anthropology **38**:137-161.

Jurgensen, T. E. 1985. Seasonal territoriality in a migratory guanaco population. MS. Iowa State University, Ames, IA.

Katoh, F., S. Hasegawa, J. Kita, Y. Takagi, and T. Kaneko. 2001. Distinct seawater and freshwater types of chloride cells in killifish, *Fundulus heteroclitus*. Canadian Journal of Zoology **277**:23-27.

Kendall, D. G. 1984. Shape-manifolds, Procrustean metrics and complex projective spaces. Bulletin of the London Mathematical Society **16**:81-121.

Kendall, D. G. 1985. Exact distributions for shapes of random triangles in convex sets. Advances of Applied Probability **17**:308-329.

Kent, J. T., and K. V. Mardia. 2001. Shape, Procrustes tangent projections and bilateral symmetry. Biometrika **88**:469-485.

Keyfitz, N. 1968. Introduction to the Mathematics of Population. Addison-Wesley, Reading, MS.

Keyfitz, N. 1977. Applied Mathematical Demography. Wiley, New York.

Kitahara, M., K. Sei, and K. Fujii. 2000. Patterns in the structure of grassland butterfly communities along a gradient of human disturbance: further analysis based on the generalist/specialist concept. Population Ecology **42**:135-144.

Klingenberg, C. P., and L. J. Leamy. 2001. Quantitative genetics of geometric shape in the mouse mandible. Evolution **55**:2342-2352.

Klingenberg, C. P., L. J. Leamy, E. J. Routman, and J. M. Cheverud. 2001. Genetic architecture of mandible shape in mice: effects of quantitative trait loci analyzed by geometric morphometrics. Genetics **157**:785-802.

Klingenberg, C. P., and G. S. McIntyre. 1998. Geometric morphometrics of developmental instability: analysing patterns of fluctuating asymmetry with Procrustes methods. Evolution **52**:1363-1375.

Krause, J. 1993. The effect of 'Schreckstoff' on the shoaling behaviour of the minnow: a test of Hamilton's selfish herd theory. Animal Behaviour **45**:1019-1024.

Krzanowski, W. J. 1993. Principals of Multivariate Analysis: A User's Perspective. Oxford University Press, New York.

Larsen, J. S., and R. D. Taber. 1980. Criteria of sex and age. Pages 143-202 *in* S. D. Schemnitz, editor. Wildlife Management Techniques Manual. The Wildlife Society, Washington, D. C.

Law, R. 1999. Theoretical aspects of community assembly. Pages 143-171 *in* J. McGlade, editor. Advanced Ecological Theory: Principles and Applications. Blackwell Science, Malden, Massachusetts.

Lawless, J. F. 1982. Statistical Models for Lifetime Data. Wiley, New York.

Lawrence, R. K. 1990. Factors influencing guanaco habitat use and group size in Torres del Paine National Park, Chile. MS. Iowa State University, Ames, IA.

Lindenfors, P., B. S. Tullberg, and M. Biuw. 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. Behavioral Ecology and Sociobiology **52**:188-193.

MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper & Row, New York.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist **101**:377-385.

MacLeod, N. 2002. Phylogenetic signals in morphometric data. *in* N. MacLeod and P. L. Forey, editors. Morphology, Shape and Phylogeny. Taylor and Francis, London.

Marcus, L. 1990. Traditional morphometrics. Pages 77-122 *in* F. J. Rohlf and F. Bookstein, editors. Proceedings of the Michigan Morphometrics Workshop. University of Michigan Museums, Ann Arbor, Michigan.

Mardia, K. V., F. L. Bookstein, and I. J. Moreton. 2000. Statistical assessment of bilateral symmetry of shapes. Biometrika **87**:285-300.

Masumoto, T. 1993. The effect of the copulatory plug in the funnel web spider, *Agelena limbata* (Araneae: Agelenidae). Journal of Arachnology **21**.

McAlpine, D. K. 1975. Combat between males of *Pogonortalis doclea* (Diptera, Platystomatidae) and its relation to structural modification. Australian Entomological Magazine **2**:104-107.

McIntosh, R. P. 1985. The background of ecology: Concept and theory. Cambridge University Press, Cambridge.

Miller, D. S., R. Masereeuw, and K. J. Karnaky. 2002. Regulation of MRP2-mediated transport in shark rectal salt gland tubules. American Journal of Physiology-Regulatory Integrative and Comparative Physiology **282**:R774-R781.

Milne, A. 1961. Definitions of competition among animals. *in Symposium for the Society for Experimental Biologists*, No. XV, Mechanisms in Biological Competition.

Monteiro, L. R., J. A. F. Diniz-Filho, S. F. dos Reis, and E. D. Araujo. 2002. Geometric estimates of heritability in biological shape. Evolution **56**:563-572.

Mosimann, J. E. 1970. Size allometry: size and shape variables with characterizations of the log-normal and generalized gamma distributions. Journal of the American Statistical Association **65**:930-945.

Moynihan, M. H., and A. F. Rodaniche. 1977. Communication, crypsis, and mimicry among cephalopods. Pages 293-302 *in* T. Sebeok, editor. How Animals Communicate. Indiana University Press, Bloomington.

Myers, C. W. 1987. New generic names for some neotropical poison frogs (Dendrobatidae). Papeis Avulsos de Zoologia Sao Paulo **36**:301-306.

Oporto, N., R. Bigatti, and Y. Larrieu E. 1984. Determinacion de edades en guanacos, en base a su denticion. Revista Argentina de Produccion Animal **4**:956-983.

Ortega, I. M. 1985. Social organization and ecology of a migratory guanaco population in southern Patagonia. MS. Iowa State University, Ames, IA.

Ortega, I. M., and W. L. Franklin. 1988. Feeding habitat utilization and reference by guanaco male groups in the Chilean Patagonia. Revist Chilena de Historia Natural **61**:209-216.

Ortega, I. M., and W. L. Franklin. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural **68**:489-500.

Otte, D., and K. Williams. 1972. Environmentally induced color dimorphisms in grasshoppers, *Syrbula admirabilis, Dicromoprha viridis,* and *Chortophaga viridifasciata*. Annals of the Entomological Society of America **65**:1154-1161.

Owings, D. H., and D. F. Hennessy. 1984. The importance of variation in sciurid visual and vocal communication. Pages 169-200 *in* J. O. Murie and G. R. Michener, editors. The Biology of Ground-dwelling Squirrels. University of Nebraska Press, Lincoln, NE.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65-74.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist **103**:91-93.

Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duvall and *Tribolium casaneum* Herbst. Ecological Monographs **18**:267-307.

Parrish, J. K. 1989. Re-examining the selfish herd: are central fish safer? Animal Behaviour **38**:1048-1053.

Pearson, K. 1901. On lines and planes of closes fit to a system of points in space. Philosophical Magazine **2**:559-572.

Perrill, S. A., H. C. Gerhardt, and R. Daniel. 1978. Sexual parasitism in the green tree frog (*Hyla cinerea*). Science **200**:1179-1180.

Pfennig, D. W., W. R. Harcombe, and K. S. Pfennig. 2001. Frequency-dependent batesian mimicry - Predators avoid look-alikes of venomous snakes only when the real thing is around. Nature **410**:323.

Pianka, E. R. 1994. Evolutionary Ecology. Pages 486 *in*. HarperCollins College Publishers, New York.

Pielou. 1969. An Introduction to Mathematical Ecology. Wiley-Interscience, New York.

Pimm, S. L. 1980. Food web design and the effect of species deletion. Oikos **35**:139-149.

Pisano, E. 1974. Estudio ecologico de la region continental sur del area andino patagonica. II. Contribucion a la fitogeografia de la zona del Parque Nacional Torres del Paine. Anales del Instituto de la Patagonia, Chile **5**:59-104.

Prexl, W. S. 1997. Differential activity of male and female juvenile guanacos in southern Chile: precursor to differential mortality? MS. Iowa State University, Ames, IA.

Puig, S., and S. Monge. 1983. Descripcion y denticion de los camelidos. Pages 51-64 *in* Estado Actual de las Investigaciones Sobre Camelidos en la Repulica Argentina. Cap. III, Buenos Aries.

Raedeke, K. 1979. Population Dynamics and Socioecology of the Guanaco (*Lama guanicoe*) of Magallanes, Chile. PhD Dissertation. University of Washington.

Reyment, R. A. 1991. Multidimensional Palaebiology. Pergamon Press, London.

Richardson, J. M. L. 2002. Burst swim speed in tadpoles inhabiting ponds with different top predators. Evolutionary Ecology Research **4**:627-642.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science **235**:167-171.

Ricklefs, R. E., and D. Schluter. 1993. Species Diversity in Ecological Communities. University of Chicago Press, Chicago.

Rijkers, T., P. Jan de Vries, T. L. Pons, and F. Bongers. 2000. Photosynthetic induction in saplings of three shade-tolerant tree species: comparing understorey and gap habitats in a French Guiana rain forest. Oecologia **125**:331-340.

Ritland, D. B., and L. P. Brower. 1991. The viceroy butterfly is not a batesian mimic. Nature **350**:497-498.

Rohlf, F. J. 1990. Fitting curves to outlines. Pages 167-177 *in* F. J. Rohlf and F. L. Bookstein, editors. Proceedings of the Michigan Morphometrics Workshop. University of Michigan Museums, Ann Arbor.

Rohlf, F. J. 1998. On applications of geometric morphometrics to studies of ontogeny and phylogeny. Systematic Biology **47**:147-158.

Rohlf, F. J. 2000. NTSYSpc. *in*. Applied Biostatistics.

Rohlf, F. J. 2002. Geometric morphometrics and phylogeny. *in* N. MacLeod and P. L. Forey, editors. Morphology, Shape and Phylogeny. Taylor and Francis, London.

Rohlf, F. J. 2003. Relative Warps (TPSrelw). *in*, SUNY at Stony Brook.

Rohlf, F. J., and J. W. Archie. 1978. Least-squares mapping using interpoint distances. Ecology **59**:126-132.

Rohlf, F. J., and L. Marcus. 1993. A revolution in morphometrics. Trends in Ecology and Evolution **8**:129-132.

Rohlf, F. J., and D. E. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic Zoology **39**:40-59.

Rüber, L., and D. C. Adams. 2001. Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. Journal of Evolutionary Biology **14**:325-332.

Sarno, R. J. 1997. Maternal expenditure and the resolution of adult-offspring conflict in the South American guanaco. PhD. Iowa State University, Ames, IA.

Sarno, R. J., W. R. Clark, M. S. Bank, W. S. Prexl, M. J. Behl, W. E. Johnson, and W. L. Franklin. 1999. Juvenile guanaco survival: management and conservation implications. Journal of Applied Ecology **36**:937-945.

Sarno, R. J., and W. L. Franklin. 1999. Population density and annual variation in birth mass of guanacos in southern Chile. Journal of Mammology **80**:1158-1162.

Sarno, R. J., W. L. Franklin, S. J. O'Brien, and W. E. Johnson. 2000a. Patterns of *mt*DNA and microsatellite variation in an island and mainland population of guanacos in southern Chile. Animal Conservation.

Sarno, R. J., W. L. Franklin, S. J. O'Brien, and W. E. Johnson. 2000b. Uso de marcadores geneticos para la conservacion de los camelidos sudamericanos silvestres. Pages 47-54 *in* Manejo Sustentable de la Vicuna y el Guanaco: Actas del Seminario Internacional realizado en la Pontifica Universidad Catolica de Chile. Pontifica Universidad Catolica de Chile, Santiago.

Sarno, R. J., W. L. Franklin, and W. S. Prexl. 2000c. Activity and population characteristics of Andean condors in southern Chile. Revista Chilena de Historia Natural **73**:3-8.

SAS Institute. 1999. SAS. *in*. SAS Institute, Inc., Cary, N.C.

SAS Institute. 2001. The MI Procedure. *in*. SAS Institute, Inc.

SAS Institute. 2002. JMP. *in*. SAS Institute Inc.

Sauer, P. R. 1984. Physical Characteristics. Pages 73-90 *in* L. K. Halls, editor. White-tailed Deer: Ecology and Management. Stackpole Books, Harrisburg, PA.

Schluter, D., T. D. Price, and P. R. Grant. 1985. Ecological character displacement in Darwin's finches. Science **227**:1056-1059.

Shine, R., M. M. Olsson, I. T. Moore, M. P. Lemaster, M. Greene, and R. T. Mason. 2000. Body size enhances mating success in male garter snakes. Animal Behaviour **59**:F4-F11.

Simberloff, D., and E. F. Connor. 1979. Q-mode and R-mode analyses of biogeographic distributions: null hypotheses based on random colonization. Pages 123-138 *in* G. P. Patil and M. L. Rosenzweig, editors. Contemporary quantitative ecology and related ecometrics. International Cooperative Publishing House, Fairland, Maryland.

Slice, D. E. 1999. Geometric motion analysis. American Journal of Physical Anthropology **Suppl. 28**:253-254.

Slice, D. E. 2001. Landmark coordinates aligned by Procrustes analysis do not lie in Kendall's shape space. Systematic Biology **50**:141-149.

Slice, D. E. 2002. The application and analysis of generalized shape trajectories. Collegium Antropologicum **26(Supplement)**:192.

Small, C. G. 1996. The Statistical Theory of Shape. Springer-Verlag, New York.

Smith, R. J. 1980. Rethinking allometry. Journal of Theoretical Biology **87**:97-111.

Strong, D. R., Jr., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984. Ecological Communities: conceptual issues and the evidence. Princeton University Press, Princeton.

Texera, W. 1973. Distribucion y diversidad de mamacfhferos y aves en la Provincia de Magallanes. Historia geologica de los generos de mamiferos nativos terrestres. Annales del Instituto de la Patagonia **4**:1-3.

Torres, H. 1992. South American Camelids: An Action Plan For Their Conservation. IUCN, Gland, Switzerland.

UNESCO. 2003. The MAB Programme: World Network of Biosphere Reserves. *in*.

Vaughan, T. A., J. M. Ryan, and N. J. Czaplewski. 2000. Mammology. Harcourt, Inc., Orlando, FL.

Wallace, A. R. 1855. On the law which has regulated the introduction of new species. Annals and Magazine of Natural History **16**.

Walther, F. R., E. C. Mungall, and G. A. Grau. 1983. Gazelles and Their Relatives: A Study in Territorial Behavior. Noyes Publications, Park Ridge, New Jersey.

White, T. D. 1991. Human Osteology. Academic Press, Inc., San Diego.

Wilson, P. 1982. An analysis of male-male aggression in guanaco male groups. MS. Iowa State University, Ames, IA.

Wilson, P. 1984. Puma predation on guanacos in Torres del Paine National Park, Chile. Mammalia **48**:515-522.

Wood, M. E. 1981. The ecology of guanaco alarm call behavior. MS. Iowa State University, Ames, IA.